# Biosystematics of the cleptoparasitic bee genus *Epeolus* Latreille and its ecological and evolutionary relationship with its hosts of the bee genus *Colletes* Latreille

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**Abstract**

Cleptoparasitic (cuckoo) bees are those that appropriate food stores from bees in other genera for their own offspring. Upwards of 15% of all bees and 28% of the family Apidae are cleptoparasitic. Despite their taxonomic richness, not much is known about the evolutionary mechanisms responsible for generating the great diversity of cuckoo bees. Moreover, studies of their evolutionary history are complicated because for many genera existing taxon concepts are problematic and taxonomic expertise is lacking. *Epeolus* Latreille (Hymenoptera: Apidae) is a widespread genus of cuckoo bees specialized on polyester bees of the genus *Colletes* Latreille (Hymenoptera: Colletidae), and belongs to the subfamily Nomadinae, the largest taxon of cleptoparasitic bees. Since *Epeolus* exhibits high host specificity, the genus can potentially serve as a model for studying the effects of bee host evolution on cleptoparasite diversification. This would first require that the taxonomy of species in *Epeolus*, which has been problematic, be resolved. Since North America has more *Epeolus* spp. than any other continent, and since others have recently or simultaneously revised species from other regions, a major objective of the present study has been to revise the species occurring in Canada and the United States. As a result, a total of 43 valid species were confirmed as present in the region, of which 15 are newly described. Additionally, 19 redundant names are newly synonymized under those of seven valid species. The next major objective has been to construct dated phylogenies for *Epeolus* and associated *Colletes* based on molecular (and in the case of *Epeolus* also morphological) data. The *Epeolus* phylogeny includes 53 ingroup and 7 outgroup taxa, whereas the *Colletes* phylogeny includes 18 ingroup taxa (species known or presumed to be hosts of particular *Epeolus* species) and two outgroup taxa (other colletids). The findings suggest that *Epeolus* originated somewhere in the Holarctic, and both genera originated sometime in the Miocene (between 19 and 17 Ma). Although there is some phylogenetic congruence between the compared *Colletes* and *Epeolus* clades, more speciation events in *Epeolus* could be linked to existing or pre-existing physical barriers than to *Colletes* diversification.

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This research project was made possible with the support and guidance of my dissertation advisor, Professor Laurence Packer. I thank Laurence for giving me every opportunity to increase my knowledge of the world of bees and travel the globe in search of them, for encouraging me to share my research with others, for continually pushing me out of my comfort zone, and for reading and editing countless drafts of text. I thank the two other members of my dissertation committee, Professor Joel Shore and Professor Amro Zayed, whose invaluable insight has helped improve this project. I am especially indebted to Amro Zayed for sharing his laboratory and equipment with me. I thank all my lab mates (past and present), including Korrawat Attasopa, Mariya Cheryomina, Leo Correia, Sheila Dumesh, Rafael Ferrari, Liam Graham, Scott MacIvor, Margarita Miklasevskaja, Spencer Monckton, James Postlethwaite, Genevieve Rowe, Bahar Salehi, and Negar Mir Sharifi. I especially thank Rafael and his family for letting me stay with them for weeks on end while writing up this dissertation, and James for helping me get the lab vehicle in good-enough condition to be driven to its final resting place in Thousand Oaks, California. During field work in the American Southwest, I frequently stayed with friends and relatives, including Alex and Ceara Chirovsky, Father Andriy and Halyna Chirovsky, my uncle Fred and aunt Olena Snow, and Chelsea and John Snow. I thank you all very much for your hospitality. I am very grateful for my parents, Fr. Andrew and Maria Onuferko, who have encouraged me to pursue my interests in the natural world throughout my entire life. I also thank my aunt Vera Szyjan for sending me countless articles and books about bees and other organisms over the years to feed my insatiable curiosity about the living planet. My sister Anna has graciously let me stay with her during my many visits to Toronto, and hasn't complained once about me filling her freezer with vials of bees. Finally, I thank my loving wife Stephanie for her never-ending support and patience throughout my many years as a graduate student.

**Statement of Authorship**

I, Thomas Onuferko, am the sole author of Chapters 1, 2, and 3 of my doctoral dissertation, entitled “Biosystematics of the cleptoparasitic bee genus *Epeolus* Latreille and its ecological and evolutionary relationship with its hosts of the bee genus *Colletes* Latreille”. Chapter 4, however, is the result of collaborative work between me and the following three individuals: Petr Bogusch, Rafael Ferrari, and Laurence Packer. This chapter, of which I am the primary author, was written entirely by me. Moreover, the results presented are based on my own analyses. However, PB, RF, and LP have all in various ways contributed significantly to this study, and should be listed as co-authors on the manuscript. It is my intention to list them as such when this paper is submitted for consideration for publication in a peer-reviewed journal after my PhD defense. All of us contributed specimens for molecular work. Although most sequences were obtained from specimens I collected during field work, PB supplied the *Epeolus* specimens from Africa and Europe, which increased the scope of this project (i.e. transformed it from a regional to global one), and LP and RF collected representatives of important North American species of *Epeolus* and *Colletes* that were used in DNA extraction and gene amplification and sequencing. Molecular work was shared between me and RF, who extracted DNA from various specimens of *Colletes* and amplified various genes from those samples. Finally, the idea of testing for co-speciation between *Epeolus* and *Colletes*, which has never before been done for any group of bees and their bee cleptoparasites, was conceived by LP. As my advisor, LP was consulted in the planning of the project at each stage and has provided me with constructive feedback on the multiple drafts of Chapter 4, which has led to its improvement. Petr Bogusch, Rafael Ferrari, and Laurence Packer all consent to being co-authors on this paper. Note that self-citations to figures are of figures in different dissertation chapters. Onuferko (2017) refers to chapter 2 and Onuferko (2018) refers to chapter 3.

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## Chapter 1: Introduction

Cleptoparasitism (a term first coined by Rothschild and Clay 1952) is a life strategy whereby one type of animal appropriates resources from another type of animal for its own offspring. Many different kinds of animals are cleptoparasitic, and among them cuckoo birds are the most well-known. A large proportion of bees species (upwards of 15% according to Batra 1984) are also cleptoparasites, and are thus commonly called cuckoo bees. Like cuckoo birds, female cuckoo bees lay eggs inside the nests of their hosts (other kinds of bees). Typically, the offspring upon hatching quickly seek out and kill the host egg or larva, though in some cleptoparasitic bees (e.g. *Sphecodes* [Hymenoptera: Halictidae]) it is the ovipositing female that destroys the host egg(s) (Michener 2007). Since the hosts of most cuckoo bees are solitary and do not provide extended brood care, their nests, once sealed with the pollen and eggs inside, are unguarded. Once the competition inside the nest has been eliminated (usually by the hospicidal first or second instar), a cuckoo bee larva will proceed to feed on the provisions put there by the host female until it is all consumed, after which the larva may diapause, pupates, ecloses, and leaves the nest as a winged adult bee (Rozen 2001).

Cleptoparasitic bees are important because they are ecologically equivalent to predators (requiring a herbivore as well as the host's flowering plants) (Sheffield et al. 2013). This means that the species that are host specific will have smaller effective population sizes and be particularly susceptible to the diploid male extinction vortex (Zayed and Packer 2005). This gives them considerable potential as environmental monitors (Sheffield et al. 2013). However, for this to happen, they have to be made identifiable, and it is well known that cuckoo bees are particularly difficult to identify (Sheffield et al. 2009, Magnacca and Brown 2012). Much of my dissertation serves to correct that difficulty.

The largest taxon of cleptoparasitic bees is the subfamily Nomadinae of the family Apidae (Hymenoptera). Among these, the bee genus *Epeolus* is particularly interesting for several reasons. First, they are diverse and widespread, represented by more than 100 species worldwide and found on all continents except Antarctica and Australia + Oceania (Ascher and Pickering 2018). Second, unlike many other cleptoparasitic bee genera, *Epeolus* is, as far as is known, entirely specialized on a single host bee genus, *Colletes* (Hymenoptera: Colletidae) (Michener 2007), whose members are commonly referred to as polyester bees because of the

polyester-like substance they secrete for the purpose of lining the insides of their nests. Third, despite their diversity they are difficult to tell apart and their taxonomy has been problematic. In light of these factors, there is both a need and opportunity to dramatically increase the knowledge about this genus, as well as to understand the evolutionary processes that have contributed to their diversity. The latter is particularly important because despite the great diversity cleptoparasitic bee species (c. 3,000 spp. divided amongst three families), no one to date has explored the evolutionary history of any group of cuckoo bees in the context of that of its host taxon and earth history events.

The objectives of this study thus threefold are: 1) to resolve the taxonomy of *Epeolus* for species occurring in North America, where its diversity is higher than anywhere else in the world, 2) to propose a comprehensive phylogeny for the genus based on molecular and morphological evidence, and 3) to explore the mechanisms responsible for promoting diversification in the genus. In doing so, I hope to increase the knowledge about this remarkable group of bees and introduce it as a comparative model for future studies on bee cleptoparasite diversification. Additional benefits of improving the taxonomic understanding of *Epeolus* are as follows. *Epeolus* are rarer than their host bees (as specialized predators are rarer than their prey). Hence, there is the potential to use them as bioindicators of the state of the environment, but that would require for there to be a means to reliably tell them apart. Cuckoo bees also tend to be quite localized, so the discovery of new species or rare species in a particular area could have implications for habitat conservation.

The first objective was tackled in two steps: 1) by revising the species of *Epeolus* occurring just in Canada and 2) by revising the members of the genus for all species occurring north of Mexico. In both cases, an integrative biosystematics approach was used. Given that cleptoparasitic bees are notoriously difficult to tell apart and that it was not initially clear if a revision of all Nearctic species could be accomplished in a PhD, the species occurring in Canada were treated first, and a revision was published separately (Chapter 2). Subsequently, the scope of the project was increased to also include all species occurring in the United States in a separate revision (Chapter 3). The second and third objectives were addressed simultaneously, with the results presented in Chapter 4. To compare the evolutionary histories of *Epeolus* and *Colletes*, cleptoparasite-host associations had to be established and representatives of both genera were collected for obtaining molecular data to construct phylogenies. For biogeographic

analyses, locality records of all included species in the phylogeny were compiled based on literature and museum records.

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## Chapter 2: Cleptoparasitic Bees of the Genus *Epeolus* Latreille (Hymenoptera: Apidae) in Canada

Thomas M. Onuferko[1]

### Abstract

The species of the cleptoparasitic (cuckoo) bee genus *Epeolus* Latreille (Hymenoptera: Apidae) occurring in Canada are revised. A total of 12 species are confirmed, with one additional species (*E. ilicis* Mitchell) listed as possibly occurring in Canada. Morphological comparisons of primary types and continuous variation within species in addition to DNA barcode sequence analysis of recently collected specimens from across the range of each species support the following proposed synonymies: *E. lanhami* Mitchell, **syn**. **n**., and *E. montanus* (Cresson), **syn**. **n**., under *E. americanus* (Cresson); *E. gabrielis* (Cockerell), **syn**. **n**., *E. geminatus* Cockerell and Sandhouse, **syn**. **n**., and *E. hitei* Cockerell, **syn**. **n**., under *E. compactus* Cresson; *E. arciferus* Cockerell, **syn**. **n**., *E. beulahensis* Cockerell, **syn**. **n**., *E. lutzi* Cockerell, **syn**. **n**., *E. lutzi dimissus* Cockerell, **syn**. **n**., and *E. pilatei* Cockerell, **syn**. **n**., under *E. minimus* (Robertson); and *E. humillimus* Cockerell, **syn**. **n**., *E. rubrostictus* Cockerell and Sandhouse, **syn**. **n**., *E. rufomaculatus* Cockerell and Sandhouse, **syn**. **n**., and *E. tristicolor* Viereck, **syn**. **n**., under *E. olympiellus* Cockerell. The synonyms of *E. americanus*, *E. compactus*, and *E. minimus* proposed here were first proposed by Richard L. Brumley in an M.Sc. thesis published in 1965, but have until now not been validated. A dichotomous identification key to the Canadian species is presented, and their biology and life history is discussed and contrasted with that of *Triepeolus* Robertson and other cuckoo bees.

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## Introduction

A high proportion (28%) of bees in the family Apidae (Hymenoptera: Apoidea) are cleptoparasites of nest-building bees (Cardinal *et al*. 2010). Cleptoparasitic (or cuckoo) bees appropriate the pollen food stores collected by females of their host species for their own offspring; the cleptoparasite invades the host nest and lays an egg in the brood cell. Subsequently, the host larva or egg (depending on the type of cleptoparasitic bee involved) is killed. Since female cleptoparasitic bees do not collect pollen to feed their brood, they lack the specialized pollen-carrying scopae characteristic of most nest-building bees. Most cleptoparasites are also wasp-like in appearance, exhibiting reduced hairiness, and typically have black and yellow and/or red colouration.

In the Nearctic region, the cleptoparasitic tribe Epeolini (Subfamily Nomadinae) is represented by *Epeolus* Latreille, *Odyneropsis* Schrottky (Griswold and Parker 1999), and *Triepeolus* Robertson (Robertson 1901). Of these, only *Epeolus* and *Triepeolus* occur in Canada, and they are the two most diverse genera in the entire tribe (Rightmyer 2004).

To date, no key to all the Canadian species of *Epeolus* has been published, although a key to the Epeolini of Ontario, the province with the greatest *Epeolus* diversity, exists (Romankova 2004). I have seen specimens from all provinces and territories in Canada except Newfoundland and Labrador and Nunavut (Map 14). I have verified locality records for 12 species in Canada (Table 1), but the key provided herein includes a thirteenth (*E. ilicis* Mitchell), which may occur in southern Ontario, whose Canadian voucher specimens (Romankova 2004) cannot be traced. The purpose of the present study is thus to provide a key to all species that might occur in Canada, and to redescribe them.

## Methods

As the sexes in this genus are for the most part monomorphic (other than for typical sexually dimorphic characters), a single identification key for adult *Epeolus* species in Canada is presented. The identification key is based on external morphological differences that should be visible in dry, pinned specimens. In addition, species redescriptions of the sex opposite that of the primary type include only the key differences between females and males.

To clarify species limits and to give additional support for new synonymies reported here, the divergence levels in a 658 bp segment of the COI mitochondrial gene (DNA barcode) (Hebert *et al*. 2003a, b) were used in conjunction with morphology. Barcoding entailed the removal of a leg (the source of genetic material) from a bee for DNA extraction and gene amplification and sequencing at the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Ontario, Canada. Barcode Index Numbers (BINs – automated code numbers given to unique barcode clusters) were assigned to sequences as short as >300 bp, although formal recognition of barcode compliant sequences requires a minimum length of 500 bp (Ratnasingham and Hebert 2007, 2013). To validate species designations of specimens and to check for contamination errors, sequences with unique BINs were compared to one another and to short, non-compliant sequences that clustered with compliant ones in a neighbour-joining (NJ) tree, based on Kimura's two-parameter distance model (Kimura 1980). Cases involving change in taxonomic status always prioritized morphological evidence over DNA barcoding, and barcoding merely confirmed what was already suspected to be continuous intraspecific variation in morphology. BINs are available for all species recorded in Canada except *E. ilicis* and are provided in the taxonomic treatment for each species. Sequences for "barcoded" specimens are published in BOLD (http://www.barcodinglife.org) in the "*Epeolus* of North America" project, and will be made available on GenBank (http://www.ncbi.nlm.nih.gov/genbank/) following a revision of all Nearctic *Epeolus* species north of Mexico.

Anatomical and taxonomic terms used generally follow Michener (2007), except I use the terms frontal and vertexal areas instead of frons and vertex, respectively, following Prentice (1998) and Dumesh and Packer (2013), as these are not clearly delimited structural features. Puncture density is quantified as the interspace (i) relative to the puncture diameter (d). MOD is an acronym for median ocellar diameter, used as a comparative measure for indicating the dimensions of smaller features, especially hair length. F with a number corresponds to one of 10 (for female) or 11 (for male) flagellomeres of the antenna. T with a number corresponds to one of six (for female) or seven (for male) exposed metasomal terga. S with a number corresponds to one of six (for female) or eight (for male) metasomal sterna. I use the term ferruginous to distinguish black or nearly black integument from that which is any of the following colours: light brown, mahogany, reddish brown, red, and rusty orange. All measurements comparing lengths and widths are based on the longest and widest margins of an anatomical feature of a

specimen at the highest magnification that would allow measurement in eyepiece micrometer units. I use the term length to describe any measurement along the longitudinal axis of a bee, and width to describe any measurement along the lateral axis, except in reference to the longitudinal extent of the transverse metasomal fasciae, for which I use the term breadth. Measurements of the scape were made excluding the radicle. Rightmyer (2008) proposed several terms specific to epeoline/nomadine bees, which I have adopted (with exceptions) and redefine here for clarity. Paramedian bands are the two longitudinal anterior lines of pale tomentum (pubescence composed of short, matted hairs) on the mesoscutum (extending posteriorly from the anterior margin of the mesoscutum but not attaining its apex) found in most *Epeolus* species. In *E. canadensis* and *E. compactus* I do not consider as paramedian bands the anteromedial patch of pale tomentum barely separated by the admedian line. The transverse bands of Rightmyer (2008) I refer to as the basal and apical metasomal fasciae. The fasciae of T1 may be connected laterally by a longitudinal band of varying width. Discal patch refers to the dark medial region of T1 covered in brown to black tomentum that may be sparser than the off-white or yellow tomentum forming the basal and apical (when present) fasciae.

Redescriptions are based on primary type specimens, although other (usually non-type sequenced) specimens were referenced for comparison and to fill in information gaps. The description of the sex opposite that of the primary type was based on the allotype or lectoallotype specimen (if available), paratypes, or non-type specimens. Specimens for study were provided by entomological institutions, museums, and university collections across Canada and the United States of America (USA), and are indicated with the following acronyms, with full names provided in parentheses: **AMNH** (American Museum of Natural History, New York, NY), **ANSP** (Academy of Natural Sciences of Drexel University, Philadelphia, PA), **BBSL** (Utah State University USDA Bee Biology and Systematics Laboratory, Logan, UT), **BIML** (Patuxent Wildlife Research Center USGS Native Bee Inventory and Monitoring Lab, Laurel, MD), **CAS** (California Academy of Sciences, San Francisco, CA), **CNC** (Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, ON), **CTMI** (Central Texas Melittological Institute, Austin, TX), **CUIC** (Cornell University Insect Collection, Ithaca, NY), **DEBU** (University of Guelph Insect Collection, Guelph, ON), **CUM** (University of Colorado Museum of Natural History in Boulder, CO), **EMEC** (University of California Essig Museum of Entomology, Berkeley, CA), **FMNH** (Field Museum of Natural History, Chicago, IL), **FSCA**

(Florida State Collection of Arthropods, Gainesville, FL), **INHS** (Illinois Natural History Survey, Champaign, IL), **KUNHM** (University of Kansas Biodiversity Institute and Natural History Museum, Lawrence, KS), **MCZ** (Harvard University Museum of Comparative Zoology in Cambridge, MA), **NCSU** (North Carolina State University Insect Museum, Raleigh, NC), **PCYU** (Packer Collection at York University, Toronto, ON), **ROM** (Royal Ontario Museum, Toronto, ON), **RSKM** (Royal Saskatchewan Museum, Regina, SK), **UCR** (University of California Entomology Research Museum, Riverside, CA), and **USNM** (U.S. National Entomological Collection, National Museum of Natural History, Washington, D.C.).

In lists of specimens examined, the records from different localities are always separated with a semi-colon. A comma between records denotes that the collection locality is the same but at least one of the following is different: date, collector, and entomological institution. With regard to specimen occurrence records, there were instances in which locality data were rather vague, particularly true of older records, and localities straddled county lines. In such cases, I omitted the county name and indicated the contents of the specimen labels. The same was true if I was unable to pinpoint an indicated locality on a Google map.

The key and redescriptions are accompanied by images taken with a Canon EOS 40D digital SLR camera using the Visionary Digital BK Plus imaging system, focus stacked in Helicon Focus, and edited in PaintShop Pro. In preparation for study and imaging, terminalia were excised, cleared in KOH for up to six hours, and ultimately stored in glycerine, later transferred to genitalia vials pinned under the associated specimens.

Range maps were constructed in RStudio (version 0.97.248) using the following packages installed in R (version 2.15.0): maptools (Bivand and Lewin-Koh 2014), raster (Hijmans 2014), rgdal (Bivand *et al*. 2014), and rgeos (Bivand and Rundel 2014). Maps of Canada and the USA were plotted using projected shapefiles obtained from Statistics Canada (2015) and the U.S. Census Bureau (2015). Points of occurrence for a particular species are based on GPS coordinates accurate to at least two decimal degrees. Using customized functions in R, continuous ranges were estimated by forming a splined convex hull polygon, a method also used for preparing distribution maps for the International Union for Conservation of Nature (IUCN 2012), of georeferenced occurrence records (from the literature and observed voucher specimens).

**Taxonomy**

Specimens of *Epeolus* species are similar to those of *Triepeolus* in general appearance, and males can be particularly difficult to distinguish. In *Epeolus*, the male pygidial plate is generally wider basally, with the lateral margins convergent toward the apex (e.g. as in *Epeolus ainsliei* Crawford [Figure 1a] and *E. olympiellus* Cockerell [Figure 1b]). In *Triepeolus*, the pygidial plate is generally comparatively narrow (e.g. as in *Triepeolus pectoralis* (Robertson) [Figure 1c] and *T. lunatus* (Say) [Figure 1d]), and its lateral margins are typically somewhat concave or sinuate. Female *Epeolus* have a very distinct sixth sternum, which is often partly visible in pinned specimens even without dissection (Figure 2a) as two convergent spatulate lateral processes bearing setae modified into pointed denticles; the processes are joined by a large lobe-like disc, which is usually not visible unless excised (Figure 2b). By contrast, S6 in female *Triepeolus* has a pair of narrow, elongate, forceps-like processes with coarse spine-like setae, separated by a disc reduced to a narrow transverse bar (Figure 2c, 2d). The apices of these processes and their long spine-like setae are often visible without dissection in pinned specimens. These morphological differences between females of *Epeolus* and *Triepeolus* are presumably related to host specialization (Rightmyer 2004) and the mechanism whereby the female oviposits into the cell wall of its host's nest or between the caps separating brood cells (Roig-Alsina 1991). The spinose setae of *Triepeolus* seem to be for digging holes in the soil walls of host cells (Torchio 1986) and/or may have a tactile function (Rightmyer 2004). In *Epeolus*, tooth-like setae on the lateral processes and the rigid attachment of these processes to the disc of the sternum indicate a saw-like function necessary for breaking through the tough polyester lining that separates brood cells and coats the cell walls of its host nest (Torchio and Burdick 1988). In at least one species of *Epeolus*, this process is aided by a glandular secretion that dissolves the polyester lining of the host nest on contact, and later resolidifies to close the gap (Torchio and Burdick 1988). Females of the two genera may be further distinguished by the pseudopygidial area – the medioapical region of T5 that generally changes slope (and may be elevated) from the rest of the tergum, and whose disc is flat or somewhat depressed and usually covered in shiny short hairs that are often uniform in length (Michener 2007). In *Epeolus*, the shape of this area is either campanulate (Figure 3a) or lunate (Figure 3b, 3c, 3d, 3e), whereas in *Triepeolus* it is more variable, and may be ovate or round (Figure 2c), quadrate, triangular, a shape intermediate

between triangular and quadrate, or a shape more complex in outline. With one notable exception, the pseudopygidial area of *Triepeolus* is always relatively longer than in *Epeolus* (Rightmyer 2008); in the unusual Mesoamerican *T. epeolurus* Rightmyer, the transverse band of metallic setae on the pseudopygidial area (Figure 3f) is remarkably similar to that of some species of *Epeolus*, but is concave rather than arched in dorsal view. Another unusual feature of *T. epeolurus* is that the pseudopygidial setae reflect silver, whereas in most *Triepeolus* they reflect a golden colour (Rightmyer 2004).

*Epeolus* is represented by 102 valid species worldwide (Integrated Taxonomic Information System on-line database, http://www.itis.gov.) [Retrieved 11.ii.2016]. Based on my own knowledge in combination with records available on Discover Life (Ascher and Pickering 2016), 45 species were until the date of this publication recognized as occurring in North America excluding Mexico and the West Indies. The first species described as being a North American *Epeolus*, *E. mercatus* Fabricius, cannot be confidently assigned to *Epeolus* or *Triepeolus*, as the original description is vague and the type material apparently has been lost (Rightmyer 2008). Therefore, the numbers above do not include *Epeolus mercatus* Fabricius. Nonetheless, it would be surprising if this species did not represent another described species in one of these two genera. Brumley (1965) described an additional seven species (all from the American Southwest), but as he did not publish his work his names cannot be formally recognized. Apparently, one of these species, occurring in Arizona and Texas, USA, had already been described by Smith (1879) from Oaxaca, Mexico (Rightmyer 2008). None of the seven "new" species, however, are known to range into Canada. Despite the diversity of *Epeolus* in North America, with more known species than any other continent, the genus is poorly understood.

Several North American species of *Epeolus* were originally described as belonging to *Phileremus* Latreille and *Triepeolus*. *Phileremus* (*Ammobates* Latreille subgenus *Ammobates* Latreille s. str. in Michener 2007) included cleptoparasitic bee species in which the fore wing has two rather than three submarginal cells. This character is variable even within species (and sometimes specimens) of *Epeolus*, and *Phileremus* contained species from a large number of genera (mostly Nomadinae), including *Ammobates*, *Ammobatoides* Radoszkowski, *Biastes* Panzer, *Epeolus*, *Dioxys* Lepeletier and Serville, *Holcopasites* Ashmead, *Melanempis* Saussure, *Neolarra* Ashmead, *Neopasites* Ashmead, and *Pasites* Jurine (Ascher and Pickering 2016).

I synonymize 14 previously proposed names under those of four valid species. *Epeolus americanus* and *E. minimus* are similar to some species that are not treated here because they occur south of Canada only. They include a cryptic species revealed by DNA barcoding (BOLD:ACZ2142) within the "*americanus* group", whose subtle morphological differences and collection date and locality record within Los Angeles County, California are shared with the holotype of *E. asperatus* Cockerell, which I have seen and examined. Also similar is the holotype of *E. melectimimus* Cockerell and Sandhouse. *Epeolus barberiellus* Cockerell is another species similar to *E. americanus*, with unique physical attributes and known to occur only in New Mexico and Texas. A species very similar to *E. minimus* is *E. banksi* (Cockerell), with unique physical attributes, and apparently restricted to parts of the mid-Atlantic and southeastern States. DNA barcode data are not yet available, but morphology suggests that specimens identified as *E. banksi* are clearly distinct from *E. minimus*. The names *E. americanus* and *E. minimus* antedate those of the abovementioned similar or cryptic species, and for the reasons stated herein I am confident that the new synonymies proposed are correct for the taxa in question, and do not apply to any other species.

**Biology**

All *Epeolus* species for which host use has been assessed are cleptoparasites of *Colletes* Latreille, the type genus of the family Colletidae (Michener 2007). The reproductive biology and immature stages of *Epeolus* were first described for *E. pusillus* Cresson in association with *Colletes ciliatoides* Stephen (Torchio 1965) and *C. compactus compactus* Cresson (Rozen and Favreau 1968). Both host species construct a single cell at the end of a lateral tunnel that branches from the meandering, mostly vertical main tunnel. Rozen and Favreau (1968) noted female *E. pusillus* flying swiftly 15–20 cm above the ground, slowing down over what presumably to them seemed to be nest entrances – one female flew quickly toward a burrow from which a host *Colletes* had previously been collected, descended, and re-emerged within a minute. When Rozen and Favreau (1968) excavated the brood cell, they found that it had an *Epeolus* egg attached, positioned between the inner and outer envelopes of the cell lining.

There is some indication that female *Epeolus* repeatedly visit and inspect the nest or nests of their host species of *Colletes*, likely to confirm the suitability of the nest site and ensure that

they are present at the right time for oviposition. For instance, Graenicher (1906) reported that upon discovering a *C. eulophi* Robertson nest (about midday), a female *E. minimus* (Robertson) began crawling over the ground with quivering wings. The female approached the nest from various angles without entering. The female *Epeolus* then perched motionless on a small plant, or twig at times, about 20 cm above the nest entrance while the female *Colletes* returned with provisions. The female *Epeolus* preened herself at that time, and again after the host female left before the *Epeolus* herself entered the nest for about one minute. The female then emerged and examined the surrounding area. The process of examining the nest entrance, perching, entering the nest, and examining the surrounding area was repeated within a particular day and on different days (confirmed by marking of the female *Epeolus* specimen). To be successful, the female *Epeolus* must avoid detection by the host. In Central Europe, Bogusch (2003) twice observed a female *C. similis* Schenck successfully defending a nest from a female *E. variegatus* (L.).

Like other Nomadinae, *Epeolus* females enter unsealed cells while the host is foraging during the nest provisioning stage. Whereas *Colletes* eggs were found to be attached to the inner polyester lining of the cell, the egg of *E. pusillus* was laid between the inner and outer polyester linings of the double-layered nest lining of its host (Rozen and Favreau 1968). Where the egg is laid depends on the host and type of nest constructed. Torchio and Burdick (1988) documented two strategies used by *E. compactus* Cresson. Its host species, *C. kincaidii* Cockerell, may reuse abandoned nests. In this case, *E. compactus* inserts its eggs between the inner lining of the burrow and residual lining (assuming it is intact) from previous nest use, because there is sufficient space and presumably also to protect the egg from getting wet. Interestingly, rates of cleptoparasitism were higher for reused nests. Torchio and Burdick (1988) found overall rates of nest parasitism of *C. kincaidii* by *E. compactus* to be as high as nearly 18%. If the nest was newly founded by the female *Colletes* host (and only a single polyester layer separates the cell from bare ground), *E. compactus* instead attaches its eggs to the caps of completed cells separating the brood cells (Torchio and Burdick 1988). Although the egg is exposed within the already completed cell, the larva hatches into the cell that was incomplete when the parent *Epeolus* oviposited. In some instances, multiple eggs may be deposited through a cell cap, but it is not known if these belong to the same or multiple female *Epeolus*. Oviposition through the cellophane-like cell lining of another colletid genus (*Scrapter* Lepeletier and Serville) has

similarly been documented in the nomadine cleptoparasitic genus *Sphecodopsis* Bischoff (Rozen and Michener 1968 – as *Pseudodichroa*). Rozen (1968) suggested that *Sphecodopsis* females puncture the lining and poke a hole in the sand outside the cell (where the egg is to be embedded) using the heavily sclerotized, median process of S6.

Rozen and Favreau (1968) observed that when the larva of *E. pusillus* hatched, it immediately found and killed the host egg. Similarly, Torchio and Burdick (1988) found that the larva of *E. compactus* killed the host egg or larva using its long, sickle-shaped mandibles, and combated the other *Epeolus* larvae in superparasitized host cells until a single survivor remained. In the case of *E. pusillus*, the rate of larval development was found to be much faster than that of the host (*C. compactus compactus* in this case), and by the time the cleptoparasite larva went into diapause, neighbouring representatives of its host species had consumed less than half of their provisions (Rozen and Favreau 1968).

Table 1. *Epeolus* in Canada and associated *Colletes* host species. The nature of the evidence for all confirmed, hypothesized (based on personal assessment), or presumed (suspected and published) associations is indicated in the Discussion section of the taxonomic treatment of each species. Unless otherwise stated, confirmed associations are based on evidence of oviposition by female *Epeolus* within a *Colletes* nest, and hypothesized and presumed associations are based on spatial and temporal co-occurrence.

| **Cleptoparasite species** | **Associated host species** | **Reference(s)** |
|---|---|---|
| *E. ainsliei* | *C. americanus* Cresson and/or *C. susannae* Swenk (presumed) | Wolf and Ascher (2009) |
| *E. americanus* | *C. consors mesocopus* Swenk (hypothesized based on shared habitat in Alaska and flight season, although at least three other Alaskan *Colletes* spp. are known) | Armbruster and Guinn (1989) |
| *E. autumnalis* | *C. compactus compactus* Cresson (presumed) | Ascher *et al*. (2014) |
| *E. bifasciatus* | *C. latitarsis* Robertson (presumed) | Mitchell (1962) |
| *E. canadensis* | Possibly *C. kincaidii* Cockerell (hypothesized) | MacKay and Knerer (1979) |
| *E. compactus* | *C. kincaidii* Cockerell (confirmed) | Torchio and Burdick (1988) |
| *E. ilicis* | *C. brimleyi* Mitchell (confirmed) | Rozen (1989) |
| *E. interruptus* | *C. aestivalis* Patton (presumed for unclear reasons) | Brumley (1965) |
| *E. lectoides* | *C. latitarsis* Robertson and *C. nudus* Robertson (presumed) | Shapiro and Droege (2010)<br>Ascher *et al*. (2014) |
| *E. minimus* | *C. eulophi* Robertson (presumed based on female *Epeolus* entering *Colletes* nest) | Graenicher (1906) |
| *E. pusillus* | *C. ciliatoides* Stephen and *C. compactus compactus* Cresson (confirmed) | Torchio (1965)<br>Rozen and Favreau (1968) |
| *E. scutellaris* | *C. simulans armatus* Patton (presumed) | Ascher *et al*. (2014) |
| *E. olympiellus* | *C. hyalinus* Provancher (hypothesized based on co-occurrence) | pers. comm. Cory Sheffield |

Key to species of *Epeolus* in Canada

1 Mesopleuron with punctures in ventrolateral half sparse (i>1d), the interspaces shining (Figure 4a, 4b); AND axilla with free portion at least as long as 1/3 its entire medial length (Figure 5a, 5b). ..... 2

- Mesopleuron with punctures in ventrolateral half dense (i≤1d) (Figure 4c) or mesopleuron rugose with punctures ill-defined, the interspaces shining or dulled by surface sculpture; IF most punctures conspicuously sparser ventrolaterally (Figure 4d), THEN axilla with free portion clearly less than 1/3 as long as its entire medial length (Figure 5c). ..... 3

2 (1) Head with frontal area bearing a pair of granulose protrusions, each located near upper mesal margin of compound eye (Figure 6a). Mesopleuron (excluding hypoepimeral area) with larger punctures (diameter of some nearly equal to diameter of lateral ocellus) in upper half than ventrolateral half (Figure 4a). T1 with broad, yellow basal fascia, T2 with similar but narrower apical fascia, metasoma otherwise without fasciae (Figure 7a). ..... ***E. bifasciatus* Cresson**

- Head with frontal area without protrusions (Figure 6b). Mesopleuron with punctures of similar size throughout (Figure 4b). T1–T4 each with conspicuous pale apical fascia (Figure 7b). .....***E. lectoides* Robertson**

3 (1) Metanotum with blunt median process, sometimes obscured by tomentum (Figure 8a). T1 with discal patch forming rounded triangle with lateral sides concave (Figure 9a). Mesopleuron with punctures in ventrolateral half sometimes so well separated (i>1d) that upper half appears to be more densely punctate than ventrolateral half (Figure 4d).....***E. interruptus* Robertson**

- Metanotum without process (Figure 8b). T1 not as above; IF discal patch triangular, THEN with convex or relatively straight sides (Figure 9b, 9c). Mesopleuron with

most interspaces between punctures small (i≤1d) (Figure 4c) or mesopleuron rugose, with punctures ill-defined. ..... 4

4 (3) Mandible without preapical angulation or tooth (Figure 10a). Axilla with free portion at least as long as 2/5 its entire medial length (usually somewhat longer) and distinctly hooked (medial margin of free portion concave and diverging from side of mesoscutellum) (Figure 5d, 5e). ..... 5

- Mandible with preapical tooth (Figure 10b) or obtuse angle appearing like a tooth (Figure 10c). Axilla with free portion clearly less than 2/5 its entire medial length and relatively straight along medial margin (Figure 5f)..... 6

5 (4) Head with preoccipital ridge joining hypostomal carina (approximately at 2/5 length of proboscidial fossa) (Figure 11a). Metasomal terga with punctures dense (i<1d) (Figure 12a). T5 with pseudopygidial area of female lunate, with apex at least twice as wide as medial length (Figure 3b)..... ***E. ainsliei*** **Crawford**

- Head with preoccipital ridge not joining hypostomal carina (Figure 11b). Metasomal terga with punctures sparser (i=1–2d), the terga appearing shiny due to larger interspaces (Figure 12b). T5 with pseudopygidial area of female distinctly campanulate, with apex less than twice as wide as medial length (Figure 3a). ..... ..... ***E. ilicis*** **Mitchell**

6 (4) Axilla with tip extending well beyond mid-length of mesoscutellum. Axilla large and robust (axillar lateral length/mesoscutellar width ratio >0.40), its lateral margin arcuate (except sometimes in *E. autumnalis*) (Figure 13a, 13b). T1 in dorsal view with discal patch so wide that the longitudinal band barely visible (its width less than half the breadth of apical fascia) (Figure 9d). ..... 7

- Axilla with tip at most extending to 1/2 length of mesoscutellum. Axilla small (axillar lateral length/mesoscutellar width ratio <0.40), its lateral margin relatively

straight (Figure 13c, 13d). T1 in dorsal view with longitudinal band at least half as wide as breadth of apical fascia (Figure 9b, 9c, 9e, 9f). ..... 9

7 (6) Axilla with tip well short of line of pale tomentum marking posterior margin of mesoscutellum; axilla and mesoscutellum entirely black (Figure 5f). ..... ..... ***E. autumnalis*** **Robertson**

- Axilla with tip attaining or surpassing line of pale tomentum marking posterior margin of mesoscutellum (may almost attain line at medioapical extent of mesoscutellum); axilla (except sometimes in *E. pusillus*) and sometimes mesoscutellum ferruginous to some degree (Figure 13a, 13b)..... 8

8 (7) Mesopleuron of male entirely obscured by white tomentum (Plate 1, Figure L). Axilla of both sexes black in part; mesoscutellum entirely black (Figure 13a). T5 with pseudopygidial area of female with apex less than twice as wide as medial length (Figure 3d). ..... ***E. pusillus*** **Cresson**

- Mesopleuron of male obscured by white tomentum only in upper half, with a large, sparsely hairy circle occupying much of ventrolateral half (Plate 1, Figure M). Axilla of both sexes partially to entirely ferruginous; mesoscutellum entirely black to entirely ferruginous (Figure 13b). T5 with pseudopygidial area of female with apex at least twice as wide as medial length (Figure 3e). ..... ***E. scutellaris*** **Say**

9 (6) F2 of female not more than 1.1 × as long as wide (Figure 14a). Pronotal lobe dark brown to black (Plate 1, Figure B). Axilla with tip close to lateral margin of mesoscutellum, with free portion at most 1/4 as long as its medial length (Figure 13c). T1 in dorsal view with longitudinal band typically more than 1.1 × as wide as breadth of apical fascia (Figure 9e). ..... ***E. americanus*** **(Cresson)**

- F2 of female at least 1.2 × as long as wide (Figure 14b). Pronotal lobe ferruginous (except sometimes in *E. minimus*) (Plate 1, Figures E, F). Axilla with tip clearly

separated from lateral margin of mesoscutellum, with free portion more than 1/4 as long as its medial length (Figure 13d). T1 in dorsal view with longitudinal band at most 1.1 × as wide as breadth of apical fascia (Figure 9b, 9c, 9f). ..... 10

10 (9) Mesoscutum with anteromedial patch of pale tomentum chevron-, horseshoe-, or V-shaped (convergent apically) (Figure 15a). T2 with fascia without lobe-like anterolateral extensions, although fascia may be broader laterally with hairs sparser basally (Figure 9b, 9c, 9f)..... 11

- Mesoscutum with paramedian band or extensively obscured by tomentum (Figure 15b, 15c). T2 with fascia with lobe-like anterolateral extensions (Figure 16a, 16b). ..... 12

11 (10) T1 with median triangular or semicircular discal patch (Figure 9b, 9c); AND metanotum with median patch of black tomentum that may be as wide as lateral patch of pale tomentum (Figure 17a) [Atlantic and Central provinces]..... ..... ***E. canadensis*** **Mitchell**

- T1 with median quadrangular discal patch (Figure 9f). Metanotum entirely covered in pale tomentum or with median interruption of sparser or darker tomentum narrower than width of lateral patch (Figure 17b) [Western provinces]. ..... ..... ***E. compactus*** **Cresson**

12 (10) T3 and T4 with fasciae not broken laterally, and complete or narrowly separated medially (Figure 16a). Labrum all black or bright-to-faded orange apically to entirely; scape, pedicel, and F1 all brown or orange in part (Figure 18a). Legs, except foreleg, typically entirely orange from trochanters to tarsi (Plate 1, Figure J). .....***E. minimus*** **(Robertson)**

- T3 and T4 with fasciae broken or at least narrowed laterally, as well as medially (Figure 16b). Labrum all black or with brown apical and lateral margins; antenna

all brown (Figure 18b). Legs dark in general (at least all coxae to femora mostly to entirely black) (Plate 1, Figure K). ..... ***E. olympiellus*** **Cockerell**

**Taxonomic treatment**

**1. *Epeolus ainsliei* Crawford, 1932 (Figures 1a, 2a, 3b, 5d, 10a, 11a, 12a; Plate 1, Figure A; Plate 2, Figure A; Plate 3, Figure A; Map 1)**

*Epeolus ainsliei* Crawford, 1932. Proc. Entomol. Soc. Wash. 34: 74 (♀).
**Primary type specimen.** Holotype ♀ (USNM, catalog number: 534035). **Collection information.** USA: Iowa: Sioux City, 15.vii.1922, C.N. Ainslie.

**Diagnosis.** Both sexes of *E. ainsliei* can be readily identified by the following combination of features: preoccipital ridge joining hypostomal carina; axilla distinctly hooked, its lateral margin arcuate; and mesopleuron densely and evenly punctate. Additionally, the following characters in combination may help separate *E. ainsliei* from other Canadian species (except perhaps *E. pusillus* and *E. scutellaris*): paramedian band present, axilla and usually also mesoscutellum ferruginous, and T2–T4 with fasciae complete.

**Redescription.** FEMALE: Length 7.8 mm; head length 2.0 mm; head width 2.7 mm; fore wing length 5.7 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, clypeus, antenna, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, mesopleuron, metapleuron, legs, metasomal terga (including pygidial plate), and metasomal sterna. Mandible with apex darker than all but extreme base. Antenna brown except scape, pedicel, and F1 orange in part. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum with orange spot anterolaterally between pronotal lobe and tegula. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket, slightly sparser on clypeus, upper paraocular and frontal areas, and vertexal area. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band.

Mesopleuron with upper half sparsely hairy, ventrolateral half sparsely covered in much shorter hairs. Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally. T1 with basal and apical fasciae and T2–T4 with apical fasciae complete but somewhat narrowed medially, T2 and T3 with facia somewhat broader laterally, and T2 with fascia with faint anterolateral extensions of sparser pale tomentum. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on impressed disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture.* Punctures dense. Labrum and clypeus with punctures equally dense (i<1d). Impunctate spot lateral to lateral ocellus absent. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d), the interspaces shining; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Mandible without preapical tooth. Labral apex with pair of small denticles preceded by carinae (difficult to see in holotype because covered in hairs; described from non-type specimens). Frontal keel present. Scape with greatest length 2.1 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.5). Preoccipital ridge joining hypostomal carina. Mesoscutellum weakly bigibbous. Axilla large, its lateral margin longer than half the mesoscutellar width (L/W ratio = 0.56) and tip extending well beyond midlength of mesoscutellum but not attaining apex; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and free portion approximately half its medial length; axilla with lateral margin arcuate and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.4); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep, well-separated punctures, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure A.

**Male genitalia.** Plate 3, Figure A.

**Discussion.** In this species, the tip of the axilla is conspicuously diverging from the side of the mesoscutellum, from which it is typically separated for half or nearly half its entire medial length. Although integument colouration is generally variable in this species, the axilla and mesoscutellum with few exceptions are entirely or almost entirely rusty orange. The discs of the metasomal terga may be entirely covered in brown to black tomentum or with tomentum of the same light colour as that comprising the metasomal fasciae. However, if pale tomentum covers the discs then it is sparser than that comprising the metasomal fasciae.

Brumley (1965) indicated that *Epeolus ainsliei* is probably conspecific with *E. lectus* Cresson, but did not personally examine the holotype of *E. lectus*, and used sketches and descriptions of it by others for comparison. I have seen the holotypes of both species, which differ considerably. Unsurprisingly, *E. lectus* is much more similar to *E. lectoides*, but is much more coarsely punctate, and T2–T4 are with complete, broader fasciae. DNA barcoding also indicates that *E. lectus* is a valid species (BOLD:ACZ8246), distinct from both *E. ainsliei* and *E. lectoides*.

HOST RECORDS: According to Wolf and Ascher (2009), one specimen was collected in association with *Colletes americanus* Cresson and *C. susannae* Swenk (possible host species) over a sandy area at Spring Green Preserve in Sauk County, Wisconsin, USA.

FLORAL RECORDS: Labels of examined voucher specimens indicate a floral association with *Dalea villosa* (Nutt.) Spreng. (Fabaceae).

**Distribution in Canada:** Southern Manitoba west to Alberta but east of the Rocky Mountains (Map 1). Possibly restricted to the Prairie Ecozone.

**DNA barcoded material.** Available. BOLD:ACZ1957. Specimens examined and sequenced.—CANADA: **Manitoba:** Spruce Woods Provincial Park (Spirit Sands Trail), 6 km N Glenboro, vii.2007, L. Packer (1♀, PCYU).

**Non-barcoded material examined.** CANADA: **Alberta:** Medicine Hat, 17.vii.1917, Sladen (1♂, BBSL), 20.viii.1916, Sladen (10♀, CNC).

USA: **Iowa:** Sioux City, 03.ix.1927, C.N. Ainslie (1♀, AMNH); **Minnesota:** 8 mi W Hitterdal (Clay County), 03.ix.1975, J.R. Powers (1♀, EMEC); **Nebraska:** Fort Robinson (Dawes County), 11.viii.1971, J.G., B.L., and K.C. Rozen (1♀, AMNH); **North Dakota:** 1 mi SE McLeod (Ransom County), 01.viii.1961, J.R. Powers (1♀, EMEC), 20.vii.1985, J.R. Powers (1♀, EMEC); 7 mi SE Sheldon (Ransom County), 26.vii.1985, J.R. Powers (1♂, EMEC); 11 mi W Walcott (Richland County), 24.vii.1963, J.R. Powers (1♀, AMNH), 30.vi.1973, J.R. Powers (1♀, EMEC), 17.vii.1981, J.R. Powers (1♀, 1♂, EMEC), 18.vii.1984, J.R. Powers (1♂, EMEC); Denbigh, 18.viii.1935, O.A. Stevens (1♀, AMNH); Sheldon, 25.vii.1949, O.A. Stevens (1♀, AMNH); **Texas:** 6 mi E Bastrop (Bastrop County), 12-13.vi.1983, W.J. Pulawski (1♂, CAS); Camp Swift – Texas Army National Guard (Bastrop County), 02.vi.2009, J.L. Neff (1♂, CTMI); San Pedro Kenedy Ranch (Kenedy County), 20.iv.2001, J.L. Neff (1♀, CTMI); Weser (Goliad County), 11.v.1952, M. Cazier, W. Gertsch, and R. Schrammel (2♀, AMNH); **Wyoming:** Dwyer, 15.vii.1966, R.J. Lavigne (1♀, USNM).

**2. *Epeolus americanus* (Cresson, 1878) (Figures 9e, 13c, 14a; Plate 1, Figure B; Plate 2, Figure B; Plate 3, Figure B; Map 2)**

*Phileremus americanus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 83 (♀, ♂); Cresson, 1916. Mem. Am. Entomol. Soc. 1: 111 (♀) [lectotype designation].
**Primary type specimen.** Lectotype ♀ (ANSP, catalog number: 2235). **Collection information.** USA: Colorado: no specific locality given, H.K. Morrison.

*Phileremus montanus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 83 (♂), **new synonymy**
**Primary type specimen.** Holotype ♂ (ANSP, catalog number: 2231). **Collection information.** USA: Nevada: no specific locality given, H. Edwards.

*Epeolus lanhami* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 450 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (CUM, catalog number: 0000041). **Collection information.** USA: Michigan: near Saline, 26.vi.1954, U.N. Lanham.

**Diagnosis.** In *Epeolus americanus*, the fore wing commonly has two submarginal cells. By contrast, in all other *Epeolus* in Canada the fore wing typically has three submarginal cells. However, in examined specimens of *E. ainsliei*, *E. minimus*, and *E. olympiellus* (including the holotype) the second or third submarginal crossvein terminates part of the way up or is missing entirely in one or both fore wings. *Epeolus americanus* can be more reliably separated from other *Epeolus* in Canada on the basis of the following features: F2 of female antenna not more than 1.1 × as long as wide, and T1 typically with narrow discal patch (longitudinal band more than 1.1 × as wide as breadth of apical fascia in dorsal view). The following features in combination help further separate this species from other *Epeolus* in Canada: pronotal lobe dark brown to black; axilla with tip inconspicuous, and axilla rather small, the tip not extending beyond midlength of mesoscutellum.

**Redescription.** FEMALE: Length 7.9 mm; head length 1.9 mm; head width 2.5 mm; fore wing length 5.7 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, and legs. Mandible with apex darker than all but extreme base. Preapical tooth as dark as mandibular apex (difficult to see in the *E. americanus* lectotype because mandible retracted; described from the *E. lanhami* holotype). Flagellum brown and (except F1) faintly lighter than conspicuously dark brown scape and brown pedicel, generally due to extensive pilosity on flagellum. Pronotal lobe dark brown to black. Tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively brown or black than reddish orange.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, ventrolateral half nearly bare. Metanotum with tomentum sparser medially, uniformly pale yellow. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. In the *E. lanhami* holotype, the patch more trapezoidal than rectangular. T2 with fascia separated medially and with anterolateral

extensions of sparser tomentum. T3 and T4 with fasciae complete medially and narrowed laterally. In the *E. lanhami* holotype and the *E. montanus* holotype, same fasciae separated medially and laterally; in the *E. lanhami* allotype, fasciae separated medially and narrowed laterally. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d), the interspaces shining; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth with blunt edge. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel present. Scape with greatest length 1.9 × greatest width. F2 not noticeably longer than wide (L/W ratio = 1.1). Preoccipital ridge not joining hypostomal carina, from which it is separated by 1.5 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin less than half as long as mesoscutellar width (L/W ratio = 0.35) and tip not extending beyond midlength of mesoscutellum; axilla with tip visible, but unattached to mesoscutellum for less than 1/4 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with two submarginal cells (true of the *E. lanhami* holotype and allotype as well). Pygidial plate mostly retracted in the *E. americanus* lectotype and the *E. lanhami* holotype and allotype, but apically truncate in non-type specimens.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, nearly as long as wide (L/W ratio = 0.8); S4 and S5 with much longer silvery to coppery subapical hairs, which individually are often darker apically; pygidial plate apically rounded, with large deep, well-separated punctures, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure B.

**Male genitalia.** Plate 3, Figure B.

**Discussion.** This species was originally placed in *Phileremus* Latreille because in the type specimens the fore wing has two submarginal cells. Subsequently, specimens in which the fore wing has three submarginal cells have been discovered, and Cockerell (1904) recognized *E. americanus* as being "to all intents and purposes *Epeolus* with two submarginal cells", even though he treated the species under the name *Phileremus americanus*. Cresson (1878) also described this species under the name *Phileremus montanus*, based on a single male specimen from Nevada. As most *Epeolus* species have been described from female type specimens, and since *E. americanus* was described from both sexes with the female having been designated as the lectotype (Cresson 1916), whereas *E. montanus* was described from only one sex, priority of the name should be given to *E. americanus*, even though both names were published simultaneously. The name *Epeolus americanus* has also become more commonly used than *E. montanus* in the literature. The types are similar except where indicated in the redescription, and the tegula of the *E. montanus* holotype is darker with sparser punctation.

*Epeolus lanhami*, with two submarginal cells, was described by Mitchell (1962), and is clearly synonymous with *E. americanus*. Except for the few abovementioned minor differences, the *E. lanhami* holotype and allotype match the present redescription of this species (based on the *E. americanus* lectotype) that includes comparisons of all three specimens. Mitchell (1962) made no mention of *E. americanus* in his taxonomic treatment of *Epeolus* of eastern USA, suggesting a lack of familiarity with the species.

Brumley (1965) identified *E. lanhami* and *E. montanus* as *E. americanus*, but also synonymized *E. asperatus* and *E. melectimimus* under this species. *Epeolus asperatus* and *E. melectimimus* appear to be the same species, native to California, USA, with distinct ornamentation on the metasomal terga and the mesopleuron and tegula more closely punctate than in *E. americanus*. Sequenced specimens most similar in morphology to the types of *E. asperatus* and *E. melectimimus* were assigned a unique BIN (BOLD:ACZ2142) separate from *E. americanus* (BOLD:AAB9110). Brumley (1965) also indicated that *E. barberiellus* is probably conspecific with *E. americanus*, but without sufficient material for comparison opted to treat the

two species as distinct, a decision with which I agree based on my own morphological comparisons.

HOST RECORDS: As is true for most *Epeolus* species, the *Colletes* host species of *E. americanus* is/are unknown. In an intensive survey of wild bees in interior and arctic Alaska, Armbruster and Guinn (1989) collected only one species/subspecies of *Colletes* (*Colletes consors mesocopus* Swenk) and one species of *Epeolus*, which they called *Epeolus* near *americanus*, in sub-arctic steppe on south-facing bluffs along the Tanana River drainage in June (1985–1986).

FLORAL RECORDS: Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Dasiphora fruticosa* (L.) Rydb. (Rosaceae) and *Lyonia ligustrina* (L.) DC. (Ericaceae). The label of one examined voucher specimen indicates an association with *Linum lewisii* Pursh (Linaceae).

**Distribution in Canada:** Known to occur in most of Canada except the high Arctic (Map 2).

**DNA barcoded material.** Available. BOLD:AAB9110. Specimens examined and sequenced.—CANADA: **Quebec:** Cap-aux-Meules (Grindstone Island, Magdalen Islands), 09.vii.2015, J. Heron and C. Sheffield (1♂, RSKM); **Yukon:** Kluane National Park and Reserve of Canada, 13.vii.2006, L. Packer (1♀, 1♂, PCYU); N. Riverdale (Whitehorse), 06.vi.2009, S.G. Cannings (3♀, PCYU); Schwatka Lake (Whitehorse), 06.vi.2009, L. Mennell (6♀, PCYU), 06.vi.2009, S.G. Cannings (2♀, 1♂, PCYU).

USA: **Colorado:** (2♀, PCYU); **Utah:** 1.46 km SE Mount Naomi, 24.vii.2008, H. Ikerd (1♀, BBSL).

**Non-barcoded material examined.** CANADA: **Alberta:** Waterton Lakes National Park, 5-14.vii.1991, H. Goulet (1♂, CNC); **British Columbia:** Atlin, 05.vii.1955, H.J. Huckel (1♂, CNC); Oliver, 04.vi.1923, C.B. Garrett (1♀, CNC); Oliver (Vaseaux Lake), 23.v.1959, R.E. Leech (1♂, CNC); **Manitoba:** Gillam, 29.vii.1950, J.F. McAlpine (1♀, CNC); **Ontario:** Black Sturgeon Lake, 10.vii.1964 (1♀, CNC); Rainy River, 24.vi.1960, S.M. Clark (4♀, 2♂, CNC); Sudbury, 07.vii.1889 (1♀, CAS); **Quebec:** Montreal Island, 24.vi.1905 (1♀, USNM); **Saskatchewan:** Athabasca Sand Dunes Provincial Park (Yakow Lake), 21-29.vi.1988, M. Polak

and M. Wood (2♀, CNC); **Yukon:** Kluane National Park and Reserve of Canada, 13.vii.2006, L. Packer (1♀, PCYU); Whitehorse (Riverdale North), 06.vii.2009, S.G. Cannings (1♀, PCYU), 30.vi.2009, S.G. Cannings (2♀, PCYU); Whitehorse (Schwatka Lake), 30.vi.2009, L. Mennell (1♀, PCYU), 26.vi.2009, L. Mennell (1♂, RSKM).

USA: **Alaska:** Big Delta, 26.vi.1951, W.R.M. Mason (1♀, CNC); Nogahabara Sand Dunes (65 mi N Galena), 1-5.vii.1989, M. Polak and D.M. Wood (1♀, 3♂, CNC); **California:** Sagehen Creek Field Station (Nevada County), 18-22.vi.1985, D.C. Darling (1♂, PCYU); **Colorado:** Gunnison County, 26.vi.2012, R. Brennan (1♀, PCYU), 10.vii.2012, S. Turner and S. Ehlman (1♀, PCYU), 13.vi.2012, R. Brennan (1♀, PCYU); Ward (Boulder County), 14.vii.1982, L. Packer (1♀, PCYU); **Idaho:** Buhl, 27.v.1929, C.F. Henderson (1♂, USNM); **Michigan:** Near Saline, 26.vi.1954, U.N. Lanham (*E. lanhami* allotype ♂ [CUM, catalog number: 0000042]); **Utah:** Pelican Canyon (Fish Lake), 26.vi.1999, L. Packer (1♀, PCYU); La Sal Mountains (Warner Lake), 29.vi.1999, L. Packer (1♀, PCYU); **Virginia:** Skyland, 26.vi.1936, R.C. Shannon (1♀, USNM).

### 3. *Epeolus autumnalis* Robertson, 1902 (Figures 4c, 5f, 10c; Plate 1, Figure C; Plate 2, Figure C; Plate 3, Figure C; Map 3)

*Epeolus autumnalis* Robertson, 1902. Entomol. News 13: 81 (♀, ♂). Webb, 1980. Ill. Nat. Hist. Surv. Bull. 32: 108 (♀) [lectotype designation (by W.E. LaBerge)].
**Primary type specimen.** Lectotype ♀ (INHS, catalog number: 44381). **Collection information.** USA: Illinois: Carlinville, C. Robertson.

**Diagnosis.** *Epeolus autumnalis* is an eastern species that can readily be identified by the following combination of features: mesopleuron closely (i≤d) and evenly punctate; axilla and mesoscutellum all black; and axilla large, but not conspicuously diverging from side of mesoscutellum, and tip extending well beyond midlength of mesoscutellum but not attaining apex. Specimens of *E. autumnalis* may attain a relatively large size (>10 mm). In this respect, in its overall dark colouration, and in general appearance, the species resembles *E. lectoides*. However, the integument of *E. lectoides* is much shinier, due in part to larger interspaces, and both species exhibit numerous other structural differences. *Epeolus autumnalis* is much more

akin to a dark *E. scutellaris*, but in *E. scutellaris* the axilla is larger, ferruginous to some degree, and attains or surpasses the line of pale tomentum demarcating the posterior margin of the mesoscutellum.

**Redescription.** FEMALE: Length 8.9 mm; head length 2.4 mm; head width 3.1 mm; fore wing length 7.5 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, and legs. Mandible with apex darker than all but extreme base. Preapical tooth lighter than mandibular apex (difficult to see in lectotype and lectoallotype; described from non-type specimens). Flagellum brown and (except F1) faintly lighter than dark brown scape and pedicel, generally due to extensive pilosity on flagellum. Pronotal lobe dark brown to black. Tegula pale ferruginous to amber. Wing membrane subhyaline and dusky in part. Legs more extensively brown than reddish orange.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron mostly bare (with tomentum rubbed off) in lectotype, but tomentum dense in lectoallotype, except for two almost entirely bare circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted, uniformly pale yellow. T1 with discal patch elliptical and very wide, the basal and apical fasciae only narrowly joined laterally. T1 and T2 with apical fasciae separated medially, and T2 with fascia without anterolateral extensions of tomentum. T3 and T4 with fasciae complete medially, and T4 with fascia narrowed laterally. T5 with two large patches of pale tomentum lateral to and contacting pseudopygidial area. T5 with pseudopygidial area lunate, its apex at least twice as wide as medial length, defined by silvery setae on impressed disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 1/3 MOD.

*Surface sculpture.* Punctures dense. Labrum with sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate dull/textured spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate

(i≤1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth blunt and obtuse. Labral apex with pair of small denticles preceded by carinae. Frontal keel present. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.6). Preoccipital ridge not joining hypostomal carina, from which it is separated by ≥2 MOD at its terminal (difficult to see in lectotype and lectoallotype; described from non-type specimens). Mesoscutellum weakly bigibbous. Axilla large, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.47) and tip extending well beyond midlength of mesoscutellum but not attaining apex; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin arcuate and carinate. Fore wing with three submarginal cells. Pygidial plate not visible in lectotype, but apically truncate in non-type specimens.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.3); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered basally and sparser apically, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure C.

**Male genitalia.** Plate 3, Figure C.

**Discussion.** The integument of this species is mostly black, and in no examined specimens are the axilla and mesoscutellum ferruginous to any degree. The pronotal lobe ranges from rusty orange to black. The axilla is large, but always well short of the posterior margin of the mesoscutellum. Although the lateral margin of the axilla is typically arcuate, it is in some specimens only very weakly curved. *Epeolus autumnalis* flies in late summer and, as its name implies, early autumn.

HOST RECORDS: An inferred *Colletes* host of *E. autumnalis*, based on size and flight season, is *C. compactus compactus* Cresson (Ascher *et al*. 2014). Personal observations support such an association. In King, Ontario, Canada, a single male specimen was collected at the same time (morning of September 24$^{th}$, 2014) as several *C. compactus* Cresson, the only temporally

co-occurring representatives of either genus sampled or observed. Also, in Toronto, Ontario, Canada, six female *E. autumnalis* were collected with many co-occurring *C. compactus* on several dates (September to October, 2015) at the same locality.

FLORAL RECORDS: Robertson (1929) reported *E. autumnalis* on *Bidens* L. (Asteraceae), *Helianthus* L. (Asteraceae), *Rudbeckia* L. (Asteraceae), and *Solidago* L. (Asteraceae). Mitchell (1962) indicated additional associations with *Aster* (now *Symphyotrichum* Nees) (Asteraceae) and *Haplopappus* Cass. (Asteraceae). Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Euthamia graminifolia* (L.) Nutt. (Asteraceae), *Leucanthemum vulgare* Lam. (Asteraceae), and *Solidago sempervirens* L. Labels of examined voucher specimens further indicate associations with *Melilotus albus* Medik. (Fabaceae), *Solidago altissima* L., *S. bicolor* L., *S. nemoralis* Aiton, and *Symphyotrichum ericoides* (L.).

**Distribution in Canada:** Atlantic and Central Canada (Map 3).

**DNA barcoded material.** Available. BOLD:AAF2361. Specimens examined and sequenced.—CANADA: **Nova Scotia:** Avonport (Kings County), 10.ix.2000, C. Sheffield (2♀, RSKM), 13.ix.2001, C. Sheffield (1♂, PCYU); **Ontario:** Black Creek Parkland (Toronto), 07.x.2015, T.M. Onuferko (1♀, PCYU).

USA: **New York:** Gardiners Island (Suffolk County), 28.ix.2007, R.G. Goelet (1♀, AMNH).

**Non-barcoded material examined.** CANADA: **Nova Scotia:** Avonport (Kings County), 10.ix.2000, C. Sheffield (1♀, PCYU), 28.viii.2000, C. Sheffield (1♀, RSKM); **Ontario:** Alderville, 01.ix.2001, S. Paiero (2♂, DEBU); Caledon Village, 02.ix.2003, J. Grixti (1♀, 1♂, PCYU), 08.ix.2003, J. Grixti (3♀, PCYU); Caledon (Forks of the Credit Provincial Park), 12.ix.1969, P. MacKay (1♂, PCYU), 29.viii.1969, P. MacKay (1♂, ROM); King, 12.ix.2000, J. Grixti (1♀, 1♂ PCYU), 29.viii.2001, M. Somers (3♂, PCYU), 21.viii.2001, M. Somers (1♂, PCYU), 16.ix.2001, M. Somers (1♀, PCYU), 23.vii.2002, J. Grixti (1♂, PCYU), 28.viii.2002, J. Grixti (1♀, 2♂ PCYU), 28.viii.2002, V. Kushnir (1♂, PCYU), 14.ix.2002, J. Grixti (1♀, PCYU), 06.ix.2003, A. Gravel (1♀, 4♂, PCYU), 06.ix.2003, J. Grixti (1♀, 1♂ PCYU); Kingston,

05.ix.1987, C. Shilton (2♀, DEBU); Niagara Falls (Niagara Whirlpool, Welland County), 11.ix.2004, M. Buck (5♂, DEBU); Toronto (York University Campus), 15.ix.2006, E. Willis (1♀, PCYU); Windsor (Ojibway Prairie), 22.ix.2001, S. Marshall (1♀, DEBU).

USA: **Illinois:** Carlinville, C. Robertson (lectoallotype ♂ [INHS, catalog number: 44382]); **Maryland:** Jug Bay Wetlands Sanctuary (Anne Arundel County), 01.x.2004, B. Hollister (1♂, BIML), 15.ix.2007, S.W. Droege (1♂, BIML); **Massachusetts:** Long Point Wildlife Refuge (West Tisbury, Dukes County), 09-10.ix.2011, P.Z. Goldstein (1♂, AMNH); Middle Moors (Nantucket County), 22.ix.2010, J.M. Karberg (1♀, AMNH); Suffolk County, 14-15.ix.2010, J. Rykken (1♂, BIML); **New York:** Gardiners Island (Suffolk County), 07.x.2005, R.G. Goelet (1♀, AMNH); Lancaster, 13.ix.1968, M.C. VanDuzee (1♂, CAS).

**4. *Epeolus bifasciatus* Cresson, 1864 (Figures 4a, 5a, 6a, 7a; Plate 1, Figure D; Plate 2, Figure D; Plate 3, Figure D; Map 4)**

*Epeolus bifasciatus* Cresson, 1864b. Proc. Entomol. Soc. Phil. 3: 38 (♂); Cresson, 1916. Mem. Am. Entomol. Soc. 1: 113 (♂) [lectotype designation].
**Primary type specimen.** Lectotype ♂ (ANSP, catalog number: 2658). **Collection information.** USA: Illinois: no specific locality given.

**Diagnosis.** *Epeolus bifasciatus* is unmistakeable among Canadian species of the genus, and both sexes can be readily identified by each of the following features that is diagnostic for the species in Canada: frontal area with pair of conspicuous granulose protrusions, each located near upper mesal margin of compound eye; punctures dense, but those of head and mesosoma sparser in some areas, larger, deep, and distinct; dorsal surface of pronotum long and distinctly angulate on anterior margin; mesoscutum without pale tomentum; and bright yellow tomentum on dorsal surface of mesosoma and metasoma.

**Redescription.** MALE: Length 7.8 mm; head length 2.3 mm; head width 2.6 mm; fore wing length 6.5 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, labrum, antenna, pronotal collar, pronotal lobe, tegula, axilla,

mesoscutellum, metanotum, and legs. Mandible with apex darker than all but extreme base. Preapical tooth lighter than mandibular apex (difficult to see in lectotype; described from non-type specimens). Antenna brown except scape, pedicel, and F1 orange. Pronotal collar, pronotal lobe, and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Pronotal collar and dorsum of metasoma with bright yellow setae. Mesoscutum without pale tomentum. Mesopleuron nearly bare, except along margins. Metanotum with tomentum narrowly interrupted medially, uniformly pale yellow. T1 with broad, medially interrupted bright yellow basal fascia. T2 with narrower, complete bright yellow apical fascia. Metasoma otherwise without fasciae, although T3–T6 with few sparsely scattered pale hairs present on apical impressed areas. S4 and S5 with long silvery to coppery subapical hairs.

*Surface sculpture.* Punctures dense, but those of head and mesosoma sparser in some areas, larger, deep, and distinct. Labrum and clypeus with similar punctation. Impunctate spot lateral to lateral ocellus absent in lectotype, but shiny spot present in non-type specimens. Mesoscutum, mesoscutellum, and axilla very coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with larger and denser (i≤1d) punctures in upper half than ventrolateral half (i>1d), the interspaces shining. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labral apex with three small denticles not preceded by carinae. Frontal keel present. Frontal area with pair of granulose protrusions, each located near upper mesal margin of compound eye. Scape with greatest length 1.7 × greatest width. F2 not noticeably longer than wide (L/W ratio = 1.1). Preoccipital ridge not joining hypostomal carina, from which it is separated by ≥2 MOD at its terminal (difficult to see in lectotype; described from non-type specimens). Pronotal collar dilated laterally to about 2 × medial length in dorsal view. Mesoscutellum moderately bigibbous, depressed along apical margin. Axilla intermediate in size, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.45) and tip extending well beyond midlength of mesoscutellum but not attaining apex; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and free portion 2/5 its medial length; axilla with lateral margin relatively straight and carinate. Fore wing with three

submarginal cells. Pygidial plate apically truncate, with large deep, closely clustered punctures, with the interspaces shining.

FEMALE: Description as for male except for usual secondary sexual characters and as follows: F2 noticeably longer than wide (L/W ratio = 1.6); T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on disc of medioapical region elevated from rest of tergum. S4 and S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 2/5 MOD); Pygidial plate with smaller punctures.

**Male hidden sterna.** Plate 2, Figure D.

**Male genitalia.** Plate 3, Figure D.

**Discussion.** Although ranging into the American Southwest, this species is more commonly known from eastern North America. *Epeolus bifasciatus* belongs to a group of Neotropical *Epeolus* so unique that they were until recently placed in their own subgenus (*Trophocleptria* Holmberg). However, in a phylogeny based on morphological characters, the subgeneric designation of this group rendered the rest of *Epeolus* paraphyletic (Rightmyer 2004). As a result, Michener (2007) proposed that the term “Trophocleptria group” be used for this monophyletic taxon until a thorough revision of the genus is made. Other similar species occur in the Neotropics and possibly along the U.S. border with Mexico, but at present only one valid species is known to occur in Canada and eastern USA.

HOST RECORDS: According to Mitchell (1962), *Colletes latitarsis* Robertson is probably the host of *E. bifasciatus*.

FLORAL RECORDS: Robertson (1929) reported *E. bifasciatus* on *Aster* (now *Symphyotrichum* Nees) (Asteraceae), *Bidens* L. (Asteraceae), *Boltonia* L'Hér. (Asteraceae), *Dalea* L. (Fabaceae), *Eryngium* L. (Apiaceae), *Eupatorium* L. (Asteraceae), *Heliopsis* Pers. (Asteraceae), *Justicia* L. (Acanthaceae), *Lythrum* L. (Lythraceae), *Pycnanthemum* Michx. (Lamiaceae), *Ratibida* Raf. (Asteraceae), *Solidago* L. (Asteraceae), *Trifolium* L. (Fabaceae), *Verbena* L. (Verbenaceae), and *Verbesina* L. (Asteraceae). Mitchell (1962) indicated additional associations with *Asclepias* L. (Apocynaceae), *Cirsium* Mill. (Asteraceae), *Coreopsis* L.

(Asteraceae), *Erigeron* L. (Asteraceae), *Helianthus* L. (Asteraceae), *Melilotus* Mill. (Fabaceae), *Nepeta* L. (Lamiaceae), *Rudbeckia* L. (Asteraceae), and *Vernonia* Schreb. (Asteraceae). Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Daucus carota* L. (Apiaceae), *Rudbeckia hirta* L., and *Melilotus officinalis* (L.) Lam. The label of one examined voucher specimen indicates an association with *Sonchus arvensis* L. (Asteraceae).

**Distribution in Canada:** Central Canada (Map 4).

**DNA barcoded material.** Available. BOLD:ADD5310. Specimens examined and sequenced.—CANADA: **Ontario:** Point Pelee National Park (Essex County), 26-27.vii.2016, R. Ferrari and T.M. Onuferko (1♀, 1♂, PCYU).

USA: **Florida:** Lake Louisa State Park (12 km S Clermont, Lake County), 05.iv.2014, K.A. Williams (1♂, FSCA).

**Non-barcoded material examined.** CANADA: **Ontario:** Caledon Village, 07.viii.2003, J. Grixti (1♀, PCYU); Grimsby, 29.vii.1944 (1♀, CNC); Hillman Marsh Conservation Area (Essex County), 03.viii.2007, S.M. Paiero (2♀, DEBU); Ottawa, 15.viii.1955, P. Taschereau (1♂, CNC); Pelee Island (Essex County), 08.vii.1965, J.C.E. Riotte and P. Hebert (1♀, ROM); Point Pelee, 29.vii.1920, N.K. Bigelow (1♂, ROM); Rondeau Park, 17.vii.1962, S.M. Clark (2♂, CNC), 18.vii.1962, S.M. Clark (2♂, CNC).

USA: **Florida:** Ormond, A.T. Solsson (1♂, AMNH); Sarasota, 20.x.1983, L. Packer (1♂, PCYU); **Illinois:** W Arthur (Moultrie County), 14.viii.1964, A.R. Moldenke (2♀, AMNH); **Maryland:** Cabin John, 18.viii.1914, J.C. Crawford (1♀, AMNH); Fulton (Howard County), 12.viii.2011, C. White (1♀, BIML); **New York:** Elba (Genesee County), 04.viii.2011, D. Green (1♂, BIML); **North Carolina:** Kill Devil Hills, 26.v.1948, K.V. Krombein (1♂, AMNH); **Pennsylvania:** Centre County, 05.viii.2016, L. Russo (1♂, BIML); **South Carolina:** Hobcaw Barony (5 km E Georgetown, Georgetown County), 11-17.ix.2007, S.M. Paiero (1♂, DEBU); **Wisconsin:** Kettle Moraine State Forest (Waukesha County), 29.viii.-28.ix.2002, C.M. Brabant (1♀, PCYU).

**5. *Epeolus canadensis* Mitchell, 1962 (Figures 9b, 9c, 17a; Plate 1, Figure E; Plate 2, Figure E; Plate 3, Figure E; Map 5)**

*Epeolus canadensis* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 444 (♀).
**Primary type specimen.** Holotype ♀ (MCZ, catalog number: 32859). **Collection information.** CANADA: Nova Scotia: Ingonish (Cape Breton Island), 07.viii.1928, G. Fairchild.

**Diagnosis.** The combination of the following features separates *Epeolus canadensis* from all other species in Canada except *E. compactus*, *E. minimus*, and *E. olympiellus*: integument mostly black; axilla (except perhaps tip) and mesoscutellum all black; legs partially ferruginous; and T1 with longitudinal band ~1 × as wide as breadth of apical fascia in dorsal view. This species most closely resembles *E. compactus*, and the character that separates both species from all other *Epeolus* in Canada is the presence of a small anteromedial patch of pale tomentum in the shape of a chevron, horseshoe, or V on the mesoscutum. By contrast, in all other Canadian species (except *E. bifasciatus*, in which the mesoscutum is without distinct pale hairs) the mesoscutum is with paramedian bands if not entirely obscured by tomentum. The fascia of T2 is without anterolateral extensions of tomentum, which are present in *E. minimus* and *E. olympiellus*. In *E. canadensis*, T1 is with a median triangular to semicircular black discal patch enclosed by pale tomentum (except for medial separation at apex), unlike the quadrangular discal patch of *E. compactus*. In Canada, both species are also be separated by geography, with *E. canadensis* not known to occur in provinces or territories west of Ontario and *E. compactus* not known to occur in provinces east of Manitoba.

**Redescription.** FEMALE: Length 8.7 mm; head length 2.1 mm; head width 2.9 mm; fore wing length 6.6 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, legs, T5, and pygidial plate. Mandible with apex and preapical tooth darker than rest of mandible. Antenna brown except scape, pedicel, and F1 extensively orange. Axilla only with tip orange. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs extensively reddish orange from tibia to tarsus.

*Pubescence.* Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with anteromedial V-shaped patch of pale tomentum. Mesopleuron with upper half densely hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum uninterrupted except for median bare patch on apical half, off white laterally and black medially. T1 with median semicircular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2–T4 with fasciae narrowed before becoming somewhat broader laterally, and T2 with fascia separated medially and without anterolateral extensions of tomentum. T3 and T4 with fasciae complete, but somewhat narrowed medially. T5 with large, nearly continuous patch of pale tomentum bordering and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labrum with pair of small subapical denticles preceded by small discreet ridges. Frontal keel present. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.2). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5 MOD at its terminal (difficult to see in holotype; described from non-type specimens). Mesoscutellum weakly bigibbous. Axilla intermediate in size, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.40) and tip not extending much beyond midlength of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, as long as wide (L/W ratio = 1.0); S4 and S5 with much longer silvery to coppery subapical hairs, which individually are often darker apically; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure E.

**Male genitalia.** Plate 3, Figure E.

**Discussion.** This species is not particularly variable, but there are differences among specimens in the width of the patch of black tomentum on the middle of the metanotum. Also, the tip of the axilla, which is typically all black, is ferruginous in some examined specimens. Although the black discal patch forms a triangle in some specimens and a semicircle in others, it is always straight basally and longest medially.

HOST RECORDS: The *Colletes* host species of *E. canadensis* is/are unknown. In the Caledon Hills of Ontario, Canada, a single female specimen was collected at the same time of year (July 9$^{th}$) as *C. kincaidii* Cockerell, the only temporally co-occurring *Colletes* species sampled from the same study area (MacKay and Knerer 1979). In a follow-up study of the same wild bee community 34 years later, Grixti and Packer (2006) rediscovered all *Epeolus* species except *E. canadensis*, and noted the near disappearance of *C. kincaidii* from the resampled site.

FLORAL RECORDS: MacKay and Knerer (1979) reported *E. canadensis* on *Melilotus albus* Medik. (Fabaceae), and Discover Life (Ascher and Pickering 2016) indicates a floral association with *Rudbeckia hirta* L. (Asteraceae). The label of one examined voucher specimen indicates an association with *Erigeron* L. (Asteraceae).

**Distribution in Canada:** Atlantic and Central Canada (Map 5).

**DNA barcoded material.** Available. BOLD:ADA0845. Specimens examined and sequenced.—CANADA: **Ontario:** 2 km N Shiloh (Wellington County), 08.viii.2004, M. Buck (1♀, DEBU);

Sixteen Mile Creek near Hwy 407 (Oakville, Halton Region), 21.viii.2004, M. Buck (1♂, DEBU).

USA: **Arizona:** AZ-366 (Mount Graham), 01.ix.2015, C. Nicholson (1♂, PCYU); **New Mexico:** Emory Pass (Gila National Forest), 16.viii.2007, M. Buck (1♂, DEBU); NM-15 Scenic (Gila National Forest), 03.ix.2015, R. Ferrari (1♂, PCYU).

**Non-barcoded material examined.** CANADA: **Nova Scotia:** Kings County, 23-24.vii.1931, C.E. Atwood (3♀, 4♂, CNC); **Ontario:** Caledon (Forks of the Credit Provincial Park), 09.vii.1968, P. MacKay (1♀, ROM), 28.vi.1965, G. Knerer (1♂, ROM); Dyer's Bay, 19.vii.1953, D.H. Pengelly (1♂, CNC); Dyer's Bay, 29.vii.1952, D.H. Pengelly (1♂, CNC); King, 10.vii.2002, V. Kushnir (1♂, PCYU); Ottawa, 07.vii.1913, F.W.L. Sladen (6♀, 9♂, CNC), 11.vii.1913, F.W.L. Sladen (2♀, CNC), 15.vii.1913, F.W.L. Sladen (1♂, CNC); Rondeau Park (Kent County), 11.vii.2005, M. Buck (1♀, DEBU); Walpole Island (Lambton County), 04.viii.2006, S.M. Paiero (1♂, DEBU); **Prince Edward Island:** Dalvay by the Sea, 05.viii.1940, J. McDunnough (1♀, CNC); **Quebec:** Gatineau (Aylmer), 03-17.viii.1924, C.H. Curran (2♀, CNC), 09.viii.1924, A.R. Graham (1♀, CNC).

USA: **Arizona:** 3 km SW Nicksville (Cochise County), 03.ix.2009, S. Dumesh and C. Sheffield (2♂, PCYU); Chiricahua Mountains (Cochise County), 24.viii.1966, V.O. Roth (1♂, AMNH); Huachuca Mountains – Ash Canyon (19 mi S Sierra Vista), 30.v.1968, R.F. Sternitzky (1♀, CNC); Huachuca Mountains – Garden Canyon (Cochise County), 1966, R.F. Sternitzky (1♀, CNC); San Francisco Peaks (Flagstaff, Coconino County), 10.viii.1934, F.E. Lutz (1♀, AMNH), 15.viii.1934, E.L. Bell (1♀, AMNH), 18-24.vii.1979, S. and J. Peck (1♀, CNC); **Arkansas:** 5 mi S Fayetteville, 10.ix.1967, R. Heitzman (1♀, FSCA); **Illinois:** Roseville, 20.viii.1940, R.I. Sailer (1♀, KUNHM); **Kansas:** Breidenthal Biological Reserve (Baldwin Woods area, Douglas County), v.-vi.1987, S.G. Reyes (1♀, KUNHM); Tuttle Creek State Park (Pottawatomie County), 06.ix.1992, B. Alexander (1♀, KUNHM); **Missouri:** Lebanon, 20.viii.1953, C.D. Michener (1♀, KUNHM); **New Mexico:** 1.5 km NE McMillan Campground (Grant County), 02.ix.2010, T.L. Griswold (1♂, BBSL); 7.8 km NE Silver City (Grant County), 30.viii.2009, T.L. Griswold (1♀, BBSL); Bear Trap Campground (28 mi SW Magdalena, Socorro County), 12.vii.1965, F., P., and M. Rindge (1♂, AMNH); Cherry Creek Campground (14 mi N Silver City, Grant County), J.E. O'Hara (4♀, 2♂, CNC), 26.v.1991, J.E. O'Hara (1♂,

CNC); **New York:** 9-Mile Creek (Ithaca), 10.vii.1937, P.P. Babiy (allotype ♂ [CUIC, catalog number: 00015611]).

**6. *Epeolus compactus* Cresson, 1878 (Figures 9f, 10b, 15a, 17b; Plate 1, Figure F; Plate 2, Figure F; Plate 3, Figure F; Map 6)**

*Epeolus compactus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 89 (♀, ♂); Cresson, 1916. Mem. Am. Entomol. Soc. 1: 115 (♀) [lectotype designation].
**Primary type specimen.** Lectotype ♀ (ANSP, catalog number: 2227). **Collection information.** USA: Texas: no specific locality given, G.W. Belfrage.

*Epeolus hitei* Cockerell, 1908. Entomologist 41: 60 (♀), **new synonymy**
**Primary type specimen.** Holotype ♀ (USNM, catalog number: 534045). **Collection information.** USA: Colorado: Copeland Park (Boulder County), 06.ix.1907, G.M. Hite.

*Triepeolus gabrielis* Cockerell, 1909. Ann. Mag. Nat. Hist. 5: 26 (♂), **new synonymy**
**Primary type specimen.** Holotype ♂ (USNM, catalog number: 534044). **Collection information.** USA: California: San Gabriel Mountains (near Pasadena), 15.vii.1909, F. Grinnell, Jr.

*Epeolus geminatus* Cockerell and Sandhouse, 1924. Proc. Calif. Acad. Sci. (4) 13: 315 (♀), **new synonymy**
**Primary type specimen.** Holotype ♀ (CAS, catalog number: 01610). **Collection information.** USA: California: Mill Creek Canyon (San Bernardino County), 12.ix.1923, E.P. Van Duzee.

**Diagnosis.** In integument colouration, pubescence, surface sculpture, and structure, this species most closely resembles *E. canadensis*, from which it can be separated on the basis of the shape of the discal patch of T1. In *E. compactus*, the discal patch is quadrangular, not triangular or semicircular as in *E. canadensis*. These species are otherwise nearly identical, and presumably sister species. For comments with regard to other similar species in Canada, see diagnosis for *E. canadensis*.

**Redescription.** FEMALE: Length 8.7 mm; head length 2.2 mm; head width 3.1 mm; fore wing length 7.1 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, legs, and pygidial plate. Mandible with apex darker than rest of mandible. Preapical tooth faintly lighter than mandibular apex (difficult to see in the *E. compactus* lectotype; described from non-type specimens). Antenna brown except scape, pedicel, and F1 extensively orange. Axilla only with tip faintly orange. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with anteromedial horseshoe-shaped patch of pale (mostly rubbed off) tomentum. Mesopleuron with upper half densely hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum uninterrupted, pale yellow laterally and darker medially on basal half. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2–T4 with fasciae narrowed before becoming somewhat broader laterally, and T2 with fascia separated medially and without anterolateral extensions of tomentum, although few sparsely scattered pale hairs present. T3 and T4 with fasciae complete, but somewhat narrowed medially. T5 with large, continuous patch of pale tomentum bordering and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 2/5 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labrum with pair of small subapical denticles preceded by small discreet ridges. Frontal keel present. Scape with greatest length 1.7 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.2). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5 MOD at its terminal (difficult to see in the *E. compactus* lectotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.40) and tip not extending much beyond midlength of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, as long as wide (L/W ratio = 1.0); S4 and S5 with much longer silvery to coppery subapical hairs, which individually are often darker apically; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure F.

**Male genitalia.** Plate 3, Figure F.

**Discussion.** *Epeolus compactus* appears to be very closely related to *E. canadensis*. I believe the two to be heterospecific on the basis of the following consistent morphological difference: T1 of *E. canadensis* has a wide median triangular to semicircular black discal patch enclosed by pale tomentum, which in *E. compactus* is distinctly quadrangular. In Canada, both species can be separated by geography, with *E. canadensis* occurring in Atlantic and Central Canada and *E. compactus* occurring in Western Canada.

*Epeolus hitei* was described as a species similar to *E. beulahensis* that exhibits the following morphological differences: the mesosoma is hairier; the discal patch of T1 is not pure black but covered in fine golden-brown pubescence; and T2 is without lateral oval spots (presumably a reference to the anterolateral extensions of the apical fascia) (Cockerell 1908).

However, no comparisons or references were made to the much more similar *E. compactus* type specimens.

Cockerell (1909) described *Triepeolus gabrielis* from a single male specimen, which was said to resemble *Triepeolus norae* Cockerell in general appearance and size, differing in the colouration of the legs and markings on T2, among other unspecified features. I have examined the holotypes of *E. hitei* and *E. gabrielis*, and the specimens both clearly exhibit the following features typical of *E. compactus*: the mesoscutum has an anteromedial patch of pale tomentum, which is chevron-shaped in the female holotype of *E. hitei* and V-shaped in the male holotype of *E. gabrielis*; T1 is with a median quadrangular black discal patch; and the fascia of T2 is without lobe-like anterolateral extensions of tomentum.

Cockerell and Sandhouse (1924) described *E. geminatus* as a distinct species, recognizable by the V-shaped patch of pale tomentum on the mesoscutum, which the authors used to separate the females from *E. rufomaculatus* (synonymized herein under *E. olympiellus*) and males from other *Epeolus* spp. in the accompanying key. I have examined the female holotype of *E. geminatus*, and the specimen with few exceptions (related to intraspecific variation in size and colour) agrees with the present redescription based on the female lectotype of *E. compactus*. Given this, and that Cockerell and Sandhouse (1924) made no comparisons of *E. geminatus* or references to *E. compactus* or *E. hitei*, it is unlikely that the three type specimens are heterospecific. Brumley (1965) first proposed that *E. gabrielis*, *E. geminatus*, and *E. hitei* are synonyms of *E. compactus*, and the present study, given molecular and morphological evidence, corroborates his discovery.

HOST RECORDS: A known *Colletes* host of *E. compactus* is *C. kincaidii* Cockerell, an association confirmed by Torchio and Burdick (1988).

FLORAL RECORDS: Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Baileya multiradiata* Harv. and A. Gray ex A. Gray (Asteraceae), *B. pleniradiata* Harv. and A. Gray ex A. Gray, *Eriogonum umbellatum* Torr. (Polygonaceae), *Melilotus officinalis* (L.) Lam. (Fabaceae), and *Palafoxia arida* B.L. Turner and Morris (Asteraceae). Labels of examined voucher specimens further indicate associations with *Encelia farinosa* A. Gray ex Torr. (Asteraceae), *Heterotheca villosa* (Pursh) Shinners (Asteraceae), and *Melilotus albus* Medik. I have personally collected this species on *Sphaeralcea* A. St.-Hil. (Malvaceae) in the American Southwest.

**Distribution in Canada:** Western Canada (Map 6).

**DNA barcoded material.** Available. BOLD:ACU6228. Specimens examined and sequenced.—USA: **California:** Hwy 20 (Mendocino County), 05.vii.2007, J. Gibbs and C. Sheffield (1♀, PCYU); **Oregon:** Hwy 140 (Jackson County), 02.vii.2007, J. Gibbs and C. Sheffield (3♂, PCYU); **Washington:** Pierce County, 24.vii.2009, C. Fimbel (1♀, PCYU).

**Non-barcoded material examined.** CANADA: **Alberta:** Lethbridge, 06.viii.1978, C.D. Michener (1♀, KUNHM); **British Columbia:** Robson, 25.vii.1955, H.R. Foxlee (1♀, CNC); Summit Creek (Creston), 28.vi.1958, H. and A. Howden (1♂, CNC); Vernon, 26.vi.1906 (1♀, CNC); **Saskatchewan:** Prince Albert, 23.vii.1959, A. and J. Brooks (1♂, CNC).

USA: **Arizona:** 1 mi NE Portal (Cochise County), 10.v.1962, W.J. Gertsch and J.A. Woods (1♂, AMNH); Douglas R/C Flying Field (Cochise County), 23.iv.2016, T.M. Onuferko (1♀, PCYU); Skeleton Canyon (Cochise County), 12.v.1977, J.G Rozen (1♀, AMNH); **California:** 1 mi S Desert Studies Center at Zzyzx Springs (San Bernardino County), 14.iv.2008, J.S. Ascher (1♂, AMNH); Monrovia (Los Angeles County), 14.vi.1921, F.E. Lutz (1♀, AMNH); Palm Springs station (Riverside County), 26.iii.1960, M. Wasbauer (1♂, AMNH); Point Molate (Richmond), 19.vii.????, F.J. Santana (1♂, FSCA); **Colorado:** (*E. compactus* paratype ♀, AMNH), (1♀, AMNH); I-70 W Silverthorne Scenic Area, 23.vii.2013, A. Payne (1♀, AMNH); Ward (Boulder County), 14.vii.1982, L. Packer (1♀, PCYU); **New Mexico:** 11 mi N Rodeo (Hidalgo County), 01.v.1969, J.G. Rozen and M.S. Favreau (5♂, AMNH); NM-146 (N Hachita, Grant County), 30.iv.2016, T.M. Onuferko (3♂, PCYU); **Oklahoma:** Garfield County, 06.vii.1962, J.F. Reinert (1♀, FSCA); **Oregon:** Hwy 140 (Jackson County), 02.vii.2007, J. Gibbs and C. Sheffield (1♂, PCYU); **Washington:** Pierce County, 24.vii.2009, C. Fimbel (1♀, PCYU); **Wyoming:** Lake Creek Camp (13 mi SE Cooke City, Montana) (Park County), 29.vii.1962, F., P., and M. Rindge (1♂, AMNH); Pacific Creek Road (Teton County), 13.viii.2013, A. Payne (1♀, AMNH); Yellowstone National Park, 09.vii.1930 (1♂, AMNH).

**7. *Epeolus ilicis* Mitchell, 1962 (Figures 3a, 5e, 11b, 12b; Plate 1, Figure G; Plate 2, Figure G; Plate 3, Figure G; Map 7)**

*Epeolus ilicis* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 448 (♀).
**Primary type specimen.** Holotype ♀ (USNM, catalog number: 534048). **Collection information.** USA: North Carolina: Holly Shelter, 30.v.1950, T.B. Mitchell.

**Diagnosis.** Among Canadian species, *E. ilicis* most closely resembles *E. lectoides* in general appearance, and especially similar are the shapes of the axilla and pseudopygidial area. Both species exhibit the following similarities: F2 of female antenna noticeably longer than wide; axilla distinctly hooked and well short of posterior margin of mesoscutellum; T1 with discal patch very wide; metasomal terga with punctures sparser (i=1–2d); and T5 with pseudopygidial area distinctly campanulate, with apex clearly less than twice as wide as medial length. In contrast to *E. lectoides*, the axilla in *E. ilicis* is more strongly angled to the side than apically, and the mesopleuron in *E. ilicis* is densely punctate, with most interspaces equally narrow above and below.

**Redescription.** FEMALE: Length 7.4 mm; head length 2.2 mm; head width 3.1 mm; fore wing length 6.0 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, mesoscutellum, and legs. Mandible with apex darker than all but extreme base. Antenna brown except scape, pedicel, and F1 orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch elliptical and very wide, the basal and apical fasciae only narrowly joined laterally. T1–T3 with apical fasciae separated medially; those of T2 and T3 somewhat broader

laterally; and T2 with fascia without anterolateral extensions of tomentum, although few sparsely scattered pale hairs present. T4 with fascia complete medially. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area campanulate, its apex less than twice as wide as medial length, defined by silvery setae on disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 2/5 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger punctures than clypeus, but punctures of both equally dense (i<1d). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d), the interspaces shining; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i=1–2d), evenly distributed on disc; the interspaces shining somewhat.

*Structure.* Mandible without preapical tooth (difficult to see in holotype; described from non-type specimens). Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel present. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.7). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal (difficult to see in holotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin nearly 2/5 as long as mesoscutellar width (L/W ratio = 0.38), but tip not extending beyond midlength of mesoscutellum; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate not visible in holotype, but apically truncate in non-type specimens.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.4); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered basally and sparser apically, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure G.

**Male genitalia.** Plate 3, Figure G.

**Discussion.** In *Epeolus ilicis*, the mesopleuron is always densely punctate, the axilla is always strongly angled to the side of the mesoscutellum, and (in females) the pseudopygidial area is always distinctly campanulate. Among specimens of this species, the metasomal fasciae are narrowly interrupted or (on T3 and T4) complete. The axilla is in many specimens partially ferruginous, and in some examined specimens the mesoscutellum is partially ferruginous as well.

HOST RECORDS: A known *Colletes* host of *E. ilicis* is *C. brimleyi* Mitchell, an association confirmed by Rozen (1989), who recovered two first instar larvae of the former species from a nest of the latter.

FLORAL RECORDS: Mitchell (1962) indicated floral associations with *Amorpha* L. (Fabaceae), *Ilex glabra* (L.) A. Gray (Aquifoliaceae), *Rhus glabra* L. (Anacardiaceae), and *Vaccinium* L. (Ericaceae), and Discover Life (Ascher and Pickering 2016) indicates an association with *Lyonia ligustrina* (L.) DC. (Ericaceae).

**Distribution in Canada:** I have not been able to verify the occurrence of *E. ilicis* in Canada, and its record in the country (Map 7) is questionable. Romankova (2004) reported this species as a new record for Canada based on three male specimens collected in southern Ontario. I have checked the holdings at DEBU, where all three are supposed to be housed, but they are missing. There are no specimens from Canada at the CNC, PCYU, ROM, and RSKM. As *E. ilicis* ranges into New York and New England, its occurrence in eastern Canada is entirely plausible. For this reason, I have not excluded *E. ilicis* from the present key, and treat it as a possible Canadian species.

**DNA barcoded material.** Unavailable.

**Non-barcoded material examined.** CANADA: None.

USA: **Georgia:** Fort Gordon (Richmond County), 25.iv.1959 (paratype ♂, NCSU); Rabun Bald (Rabun County), 14.vii.1957, J.G. Chillcott (1♀, CNC); Satolah (Rabun County), 01.vii.1957, J.R. Vockeroth (1♀, CNC), 04.vii.1957, W.R.M. Mason (1♂, CNC); St. Catherines Island (Liberty County), 10-14.iv.1991, J.G. Rozen, E. Quinter, and A. Sharkov (1♀, AMNH);

**Massachusetts:** Amherst, Spring 1929, L.A. Carruth (1♂, USNM); **North Carolina:** Highlands, 27.vi.1957, W.R.M. Mason (1♀, CNC); Highlands (Horse Cove), 25.vi.1957, W.R.M. Mason (1♂, CNC), 27.vi.1957, J.R. Vockeroth (4♂, CNC); Highlands (Whiteside Mountain), 11.vii.1937, T.B. Mitchell (paratype ♂, NCSU), 29.vi.1957, W.R.M. Mason (1♀, CNC), 29.vi.1957, J.R. Vockeroth (1♀, CNC); Wayah Bald (Macon County), 06.vii.1957, W.R.M. Mason (1♀, CNC); **South Carolina:** Hunting Island State Park (Beaufort County), 08.iv.1963, J.G. and B.L. Rozen (1♂, AMNH); McClellanville, 12.v.1944, H. and K. Townes (paratype ♂, NCSU), 19.v.1944, H. and G. Townes (paratype ♂, NCSU); Mountain Rest, 14.vi.1957, W.R.M. Mason (1♂, CNC).

**8. *Epeolus interruptus* Robertson, 1900 (Figures 4d, 5c, 8a, 9a; Plate 1, Figure H; Plate 2, Figure H; Plate 3, Figure H; Map 8)**

*Epeolus interruptus* Robertson, 1900. Trans. Acad. Sci. St. Louis 10: 55 (♀).
**Primary type specimen.** Holotype ♀ (INHS, catalog number: 44384). **Collection information.** USA: Illinois: Carlinville, C. Robertson.

**Diagnosis.** The distinguishing features that separate *E. interruptus* from all other *Epeolus* in North America include the presence of a blunt median process on the metanotum, which is partially if not entirely obscured by tomentum, and the very wide discal patch of T1 uniquely forming a rounded triangle with concave lateral sides. Other defining attributes include the following in combination: F2 of female antenna noticeably longer than wide; mesoscutum with paramedian band; axilla with tip inconspicuous, and axilla rather small and tip not extending beyond midlength of mesoscutellum; and T1–T4 with basal and apical fasciae interrupted medially.

**Redescription.** FEMALE: Length 7.6 mm; head length 2.3 mm; head width 2.8 mm; fore wing length >6.6 mm (margins of both very worn in holotype).

*Integument colouration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, mesoscutellum, legs, and pygidial plate. Mandible with apex darker than all but extreme base. Preapical tooth faintly

lighter than mandibular apex (difficult to see in holotype; described from non-type specimens). Antenna brown except scape, pedicel, and F1 orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum denser medially except for bare patch on apical half, uniformly off white. T1 with discal patch very wide, the basal and apical fasciae only narrowly joined laterally and forming rounded triangle with lateral sides concave. T1 with basal fascia interrupted medially, T1–T4 with apical fasciae interrupted medially and narrowed before becoming somewhat broader laterally, and T2 with fascia with anterolateral extensions of sparser tomentum. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 1/3 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger punctures than clypeus, but punctures of both more or less equally dense (i<1d). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with denser (i≤1d) punctures in upper half than ventrolateral half (i>1d), the interspaces shining. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel present. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin less than half as long as mesoscutellar width (L/W ratio = 0.38) and tip not extending beyond midlength of mesoscutellum; axilla with tip visible, but unattached to mesoscutellum for less than 1/3 its medial length; axilla with lateral margin

relatively straight and without carina. Metanotum with blunt median process obscured by tomentum. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.2); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep, closely clustered punctures, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure H.

**Male genitalia.** Plate 3, Figure H.

**Discussion.** *Epeolus interruptus* is an enigmatic species, and does not closely resemble any other in Canada. Punctation density of the mesopleuron is generally variable (1≥i>1), showing continuous variation with no consistent geographic pattern among specimens. Although the axilla and mesoscutellum are typically all-ferruginous, in some examined specimens they are partially to entirely black. I do not know of very many records of this species in Canada, and presumably it is uncommon in the northern part of its range.

HOST RECORDS: According to Brumley (1965), the *Colletes* host of *E. interruptus* is *C. aestivalis* Patton, but no details were provided with regard to the basis of this apparent association. In Cache County, Utah, USA, several *E. interruptus* specimens were collected with many co-occurring *C. willistoni* Robertson (all from *Physalis longifolia* Nutt. [Solanaceae]) on several dates in July 2015 at the same locality, suggesting a different host-parasite association (T. Griswold, personal communication, 2015).

FLORAL RECORDS: Robertson (1929) reported *E. interruptus* on *Coreopsis* L. (Asteraceae), *Krigia* Schreb. (Asteraceae), *Psoralea* L. (Fabaceae), and *Rudbeckia* L. (Asteraceae). Mitchell (1962) indicated additional associations with *Chrysanthemum* L. (Asteraceae) and *Trifolium* L. (Fabaceae), and Discover Life (Ascher and Pickering 2016) indicates a floral association with *Baccharis* L. (Asteraceae). Labels of examined voucher specimens further indicate associations with *Kallstroemia* Scop. (Zygophyllaceae), *Melilotus albus* Medik. (Fabaceae), and *Physalis longifolia*.

**Distribution in Canada:** Central to Western Canada, east of the Rocky Mountains (Map 8).

**DNA barcoded material.** Available. BOLD:ACZ9058. Specimens examined and sequenced.—USA: **Arizona:** Geronimo Trail at Sycamore Creek (Cochise County), 28.viii.2016, L. Packer (3♀, 2♂, PCYU); **Utah:** 1 km W Hyrum Dam (Cache County), 19.vii.2015, T.L. Griswold (1♂, BBSL); **Virginia:** Lancaster (Lancaster County), 02-10.vi.2011, A.W. Hook (1♀, CTMI).

**Non-barcoded material examined.** CANADA: **Manitoba:** Aweme, 01.vii.1925, B.D. Bird (6♀, CNC); **Ontario:** Ottawa, 29.vii.1947, W.R.M. Mason (1♀, CNC).

Mexico: **Baja California:** San Vicente, 08.vii.1963, P.D. Hurd (1♂, EMEC); USA: **Arizona:** 1 mi E Douglas (Cochise County), 16.viii.1962, M. Statham (1♀, AMNH); 14 mi SW Apache (Cochise County), 04.viii.1961, J.G. Rozen (1♂, AMNH); 15 mi SW Apache (Cochise County), 23.viii.1997, B. McAdams and J.G. Rozen (1♀, AMNH); 18 mi SW Apache (Cochise County), 18.viii.1994, J.S. Ascher and J.G. Rozen (1♂, AMNH); 26 mi E Douglas, 29.viii.2013, G. Rowe (1♂, PCYU); AZ-80 (Cochise County), 03.v.2012, A. Payne and J.G. Rozen (1♂, AMNH); **Iowa:** Sioux City, 10.vii.1920, C.N. Ainslie (1♀, AMNH); **Louisiana:** C.F. Baker (1♂, USNM); **Nebraska:** Cedar Point Biological Station (Keith County), 11-18.vii.1968, J.G. Rozen and E. Quinter (1♀, AMNH); **New Mexico:** 1.8 km NW Manzano (Cañon Nuevo), 02.viii.2009, T.L. Griswold (1♂, BBSL); 4 mi N NW Las Vegas, 02.vii.1946, B.A. Maina (1♂, FMNH); **Texas:** 6 mi W Uvalde (Uvalde County), 22.iii.2001, J.L. Neff (1♀, CTMI); Chaparral Wildlife Management Area (Dimmit County), 16-18.iv.1993, A.W. Hook (1♀, CTMI); San Antonio, H.B. Parks (1♀, AMNH); **Utah:** 1 km W Hyrum Dam (Cache County), 05.vii.2015, T.L. Griswold (1♂, BBSL).

**9. *Epeolus lectoides* Robertson, 1901 (Figures 4b, 5b, 6b, 7b; Plate 1, Figure I; Plate 2, Figure I; Plate 3, Figure I; Map 9)**

*Epeolus lectoides* Robertson, 1901. Can. Entomol. 33: 231 (♀).
**Primary type specimen.** Holotype ♀ (INHS, catalog number: 44383). **Collection information.** USA: Illinois: Carlinville, C. Robertson.

*Epeolus semilectus* Cockerell, 1907. Entomologist 40: 136 (♂).
**Primary type specimen.** Holotype ♂ (USNM, catalog number: 534053). **Collection information.** USA: Virginia: Falls Church, 04.vii.????, N. Banks.

**Diagnosis.** Although separated from *E. bifasciatus* in the key, this species most closely resembles *E. ilicis* among Canadian *Epeolus*, particularly in the campanulate shape of the pseudopygidial area of T5 in the female. *Epeolus ilicis* and *E. lectoides* exhibit several structural similarities (F2 of female antenna noticeably longer than wide, axilla distinctly hooked, and metasomal terga with sparse punctation), but in contrast to *E. ilicis* the mandible of *E. lectoides* is with a preapical tooth, the ventrolateral half of the mesopleuron of *E. lectoides* is sparsely punctate (i>1d), and the axilla of *E. lectoides* is angled posteriorly and its tip extends well beyond the midlength of the mesoscutellum.

**Redescription.** FEMALE: Length 8.7 mm; head length 2.2 mm; head width 3.1 mm; fore wing length 7.2 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, and legs. Mandible with apex darker than all but extreme base. Preapical tooth faintly lighter than mandibular apex. Flagellum brown and (except F1) faintly lighter than partially dark brown (otherwise orange) scape and F1 and entirely dark brown pedicel, generally due to extensive pilosity on flagellum. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline and dusky in part. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum tarnished in the *E. lectoides* holotype, but white and densest around antennal socket in non-type specimens. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white setae. Mesoscutum with paramedian band. Mesopleuron with upper half sparsely hairy, ventrolateral half nearly bare. Metanotum with tomentum uninterrupted except for median bare patch on apical half, uniformly white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally. T1 with basal and apical fasciae and T2–T4 with apical fasciae separated medially, those of T2 and T3 somewhat broader laterally, and T2 with fascia with faint anterolateral extensions of sparser pale

tomentum. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area campanulate, its apex less than twice as wide as medial length, defined by silvery setae on impressed disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 2/5 MOD.

*Surface sculpture.* Punctures dense, but those of head and mesosoma sparser in some areas, larger, deep, and distinct. Labrum with larger punctures than clypeus, but punctures of both equally dense (i<1d). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla very coarsely and densely rugose-punctate; the interspaces shining. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with denser (i≤1d) punctures in upper half than ventrolateral half (i>1d), the interspaces shining. Metasomal terga with punctures very fine, dense (i=1–2d), evenly distributed on disc; the interspaces shining somewhat.

*Structure.* Preapical tooth blunt and obtuse. Labrum with pair of small subapical denticles preceded by small discreet ridges. Frontal keel present. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.6). Preoccipital ridge not joining hypostomal carina, from which it is separated by less than 1 MOD at its terminal (difficult to see in the *E. lectoides* holotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla large, its lateral margin half as long as mesoscutellar width (L/W ratio = 0.51) and tip extending well beyond midlength of mesoscutellum but not attaining apex; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin arcuate (somewhat) and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.4); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces somewhat dull.

**Male hidden sterna.** Plate 2, Figure I.

**Male genitalia.** Plate 3, Figure I.

**Discussion.** Mitchell (1962) synonymized *Epeolus semilectus* under *Epeolus lectoides*. I have examined the male holotype specimen of *E. semilectus*, and agree with Mitchell's treatment. Excluding sex-specific characters, the redescription of the *E. lectoides* holotype with few exceptions (related to intraspecific variation in size and colour) applies equally well to that of *E. semilectus*. Cockerell (1907) suggested that *E. semilectus* is a "geographical race" of *E. lectoides*, but one in which only a single metasomal fascia is interrupted medially. In fact, all metasomal fasciae of the *E. semilectus* holotype are narrowly interrupted medially except for the apical fascia of T1, which is more widely interrupted than the other fasciae.

HOST RECORDS: Inferred *Colletes* hosts of *E. lectoides*, based on co-occurrence, are *C. latitarsis* Robertson (Shapiro and Droege 2010) and *C. nudus* Robertson (Ascher *et al*. 2014). It should be noted, however, that the single specimen of *C. latitarsis* was collected two months earlier than the specimen of *E. lectoides*, and at a different site within the larger study area around the Cove Point Liquefied Natural Gas Site in Calvert County, Maryland, USA.

FLORAL RECORDS: Robertson (1929) reported *E. lectoides* on *Pycnanthemum* Michx. (Lamiaceae). Mitchell (1962) indicated additional associations with *Ceanothus* L. (Rhamnaceae), *Cephalanthus* L. (Rubiaceae), *Helenium* L. (Asteraceae), *Hypericum* L. (Hypericaceae), and *Rhus* L. (Anacardiaceae). Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Achillea millefolium* L. (Asteraceae), *Lycopus* L. (Lamiaceae), *Mentha X piperita* L. (Lamiaceae), *Pluchea odorata* (L.) Cass. (Asteraceae), *Tanacetum vulgare* L. (Asteraceae), and *Teucrium canadense* L. (Lamiaceae). Labels of examined voucher specimens further indicate associations with *Cryptantha cinerea* (Greene) Cronquist (Boraginaceae) and *Dalea villosa* (Nutt.) Spreng. This species has been collected on *Melilotus albus* Medik. (Fabaceae) in Point Pelee National Park, Ontario, Canada (R. Ferrari, personal communication, 2016).

**Distribution in Canada:** Central Canada (Map 9).

**DNA barcoded material.** Available. BOLD:AAF2273. Specimens examined and sequenced.—CANADA: **Ontario:** Point Pelee National Park (Essex County), 25-30.vii.2003, Paiero and Cheung (1♂ DEBU); Rondeau Park, 01.viii.2005, M. Buck (1♂, DEBU).

USA: **Nebraska:** Mahoney State Park (Cass County), 2-3.vii.2011, J. Droegemueller (1♂, BIML); **South Carolina:** (1♀, 2♂, PCYU).

**Non-barcoded material examined.** CANADA: **Ontario:** Pinery Provincial Park, 25-28.vi.1986, L. Packer (1♂, PCYU); Point Pelee, 02.viii.1920, N.K. Bigelow (1♀, ROM), 04.viii.1920, N.K. Bigelow (1♀, 1♂, ROM), 08.viii.1920, N.K. Bigelow (1♀, ROM), 13.viii.1920, N.K. Bigelow (4♂, ROM), 29.vii.2003, M. Buck (6♂, DEBU); Point Pelee National Park (Essex County), 25-30.vii.2003, Paiero and Cheung (1♀, 1♂ DEBU), 26-27.vii.2016, R. Ferrari and T.M. Onuferko (7♀, 10♂, PCYU); Rondeau Park, 29.vii.-14.viii.2003, S.M. Paiero and S.A. Marshall (3♀, DEBU), 14.viii.2003, S.M. Paiero (1♀, DEBU).

USA: **Kansas:** 0.5 mi N & 3.3 mi E Crestline (Cherokee County), 26.vi.1965, G.F. Hevel (1♂, USNM); Breidenthal Biological Reserve (15 mi SE Lawrence, Douglas County), 30.vi.1979, R.J. McGinley (1♂, USNM); **Maryland:** 4 mi SE Salisbury (Wicomico County), 30.viii.2007, M. Buck (1♀, DEBU); Blackwater National Wildlife Refuge (Dorchester County), 12.viii.2015, S.W. Droege (1♂, BIML); **New Jersey:** Edwin B. Forsythe National Wildlife Refuge, 26-27.viii.2008, A. Mortens and D. Conrad (1♀, BIML); **New York:** Gardiners Island (Suffolk County), 17-23.viii.1918 (1♂, AMNH), 04.viii.2007, J.S. Ascher, R.G. Goelet, and J.G. Rozen (1♂, AMNH), 25.viii.2008, R.G. Goelet (1♀, AMNH); **North Carolina:** Kill Devil Hills, 30.vi.1950, K.V. Krombein (1♀, AMNH), 04.vii.1950, K.V. Krombein (1♀, AMNH); **North Dakota:** Sheldon, 25.vii.1949, O.A. Stevens (1♀, AMNH); **South Carolina:** Carolina Sandhills National Wildlife Refuge (Chesterfield County), 07.ix.2006, S.W. Droege (1♀, BIML); **Virginia:** Chincoteague National Wildlife Refuge (Accomack County), 1-2.vii.2006, S.W. Droege (1♀, 2♂, BIML).

**10. *Epeolus minimus* (Robertson, 1902) (Figures 8b, 13d, 15b, 16a, 18a; Plate 1, Figure J; Plate 2, Figure J; Plate 3, Figure J; Map 10)**

*Triepeolus minimus* Robertson, 1902. Entomol. News 13: 81 (♀).
*Argyroselenis minima* Robertson, 1903. Can. Entomol. 35: 284.

**Primary type specimen.** Holotype ♀ (INHS, catalog number: 62276). **Collection information.** USA: Illinois: Carlinville, C. Robertson.

*Epeolus beulahensis* Cockerell, 1904. Ann. Mag. Nat. Hist. 13: 40 (♀), **new synonymy**
**Primary type specimen.** Holotype ♀ (USNM, catalog number: 534040). **Collection information.** USA: New Mexico: Beulah, 11.vii.????, Cockerell.

*Epeolus lutzi* Cockerell, 1921. Am. Mus. Novit. 23: 16 (♂), **new synonymy**
**Primary type specimen.** Holotype ♂ (AMNH, catalog number: 25098). **Collection information.** USA: Colorado: Walsenburg, 14.vi.1919.

*Epeolus lutzi dimissus* Cockerell, 1921. Am. Mus. Novit. 23: 16 (♀), **new synonymy**
**Primary type specimen.** Holotype ♀ (AMNH, catalog number: 25099). **Collection information.** USA: Colorado: Leadville, 03-05.viii.1919.

*Epeolus arciferus* Cockerell (in Cockerell and Sandhouse, 1924). Proc. Calif. Acad. Sci. (4) 13: 319 (♀), **new synonymy**
**Primary type specimen.** Holotype ♀ (CAS, catalog number: 01614). **Collection information.** USA: California: Pacific Grove (Monterey County), ix.1920, F.E. Blaisdell.

*Epeolus pilatei* Cockerell (in Cockerell and Sandhouse, 1924). Proc. Calif. Acad. Sci. (4) 13: 320 (♀), **new synonymy**
**Primary type specimen.** Holotype ♀ (CAS, catalog number: 01615). **Collection information.** USA: California: San Pedro, 25.x.1909, G.R. Pilate.

*Epeolus eastwoodae* Cockerell, 1937. Pan-Pac. Entomol. 13: 149 (♂).
**Primary type specimen.** Holotype ♂ (CAS, catalog number: 04651). **Collection information.** USA: California: Cuyler's Cove (San Miguel Island), 27.vii.1937, Cockerell.

**Diagnosis.** Among Canadian species, *E. minimus* most closely resembles *E. olympiellus*, and the two can be difficult to distinguish from one another where their ranges overlap. *Epeolus minimus*

can be readily distinguished from all other *Epeolus* in Canada except *E. olympiellus* by the following combination of features: F2 of female at least 1.2 × as long as wide; mesoscutum with paramedian band (if not entirely obscured by pale tomentum); mesopleuron closely and evenly punctate; axilla with lateral margin relatively straight, axilla with tip clearly separated from lateral margin of mesoscutellum and not extending much beyond midlength of mesoscutellum; axilla (except perhaps tip) and mesoscutellum all black; and T2 with fascia with anterolateral extensions of tomentum. *Epeolus minimus* typically exhibits reddish orange colouration on the labrum (apically or entirely), antenna, and quite extensively on the legs. In *E. olympiellus*, the fasciae of T3 and T4 are typically entirely broken or greatly narrowed laterally, a state not observed in specimens of *E. minimus*.

**Redescription.** FEMALE: Length 7.7 mm; head length 2.0 mm; head width 2.6 mm; fore wing length 6.2 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, legs, and pygidial plate. Mandible with apex and preapical tooth darker than all but extreme base. Flagellum brown and (except F1) faintly lighter than partially dark brown (otherwise orange) scape, pedicel, and F1, generally due to extensive pilosity on flagellum. Axilla only with tip orange in the *E. minimus* holotype (axilla all black in the *E. beulahensis* holotype). Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Tomentum mostly rubbed off on clypeus of the *E. minimus* holotype, but dense in the *E. beulahensis* holotype. Upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron in both the *E. minimus* and *E. beulahensis* holotypes with dense tomentum, except for two sparsely hairy to entirely bare circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted, uniformly off white. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2 with fascia separated medially and with anterolateral extensions of equally dense tomentum. T3 and T4 with fasciae complete, but

somewhat narrowed medially. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex at least twice as wide as medial length, defined by silvery setae on impressed disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 2/5 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate spot present lateral to lateral ocellus (dull in the *E. minimus* holotype, but shiny in the *E. beulahensis* holotype). Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron largely obscured by tomentum, but ventrolateral half densely punctate (i<1d) to rugose where exposed; mesopleuron with punctures more or less equally dense throughout where exposed. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel present. Scape with greatest length 1.7 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by 1.5 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.40) and tip not extending much beyond midlength of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, not noticeably longer than wide (L/W ratio = 1.1); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure J.

**Male genitalia.** Plate 3, Figure J.

**Discussion.** This species, originally placed in *Triepeolus*, is very widely distributed in North America. Following its transfer to the now defunct genus *Argyroselenis* Robertson, the first record of its correct transfer to the genus *Epeolus* I have seen in the literature is in Mitchell (1962), but the change in taxonomic status was not listed as a new combination. Given its variability, as well as its similarity to *E. banski* (in eastern USA), *E. olympiellus* (in western North America), and a Californian species that has yet to be formally recognized, *E. minimus* has been the subject of much taxonomic confusion. Brumley (1965) proposed 10 unpublished synonymies of *E. minimus*, but discussed several intraspecific groups that could not be separated logically or consistently. Although opting to consider them as conspecific, Brumley (1965) acknowledged that further study may indicate that some of these groups represent distinct species. Barcode sequencing to date has shown there to be at least three valid species in the "*minimus* group", one of which (*E. olympiellus*) does not appear to occur east of the Rocky Mountains. With few exceptions (related to intraspecific variation in size and colour), the *E. beulahensis* holotype agrees with the present redescription based on the *E. minimus* holotype, which compares and contrasts the two specimens. In Cockerell's (1904) original description, no comparisons of the *E. beulahensis* holotype were made to *E. minimus*. Cockerell (1904) suggested that *E. beulahensis* is closely allied to *E. autumnalis* (a very different species). Although barcode sequences are currently lacking for specimens from the two type localities of *E. beulahensis* and *E. minimus* (in Beulah, New Mexico and Carlinville, Illinois, respectively), the same BIN was assigned to specimens ranging widely from Yukon to Colorado and east to southern Ontario.

Additionally, Cockerell (1921) described this species under the names *E. lutzi* and *E. lutzi dimissus*. I have examined the types of both specimens, which exhibit the following features associated with *E. minimus*: labrum ferruginous apically; legs, except foreleg, orange from trochanters to tarsi; T2 with lobe-like anterolateral extensions; and T3 and T4 with fasciae complete. The type localities (both in Colorado) fall within the range of sequenced specimens.

Brumley (1965) discussed coastal and insular Californian types of *Epeolus* in the "*minimus* group", for which the names *E. arciferus* Cockerell, *E. eastwoodae* Cockerell, and *E. pilatei* Cockerell have been applied. *Epeolus eastwoodae* has since been synonymized under *E. minimus* by Rust (1984). The three type specimens from California, which I have examined, are very similar to one another, and their integument (including that of the pronotal lobe) is virtually

all black. However, the pattern of pubescence on the metasoma is like that of the *E. minimus* holotype (the fasciae of T3 and T4 are complete or narrowly interrupted medially, and not broken or conspicuously narrowed laterally). There is continuous variation in the degree of reddish orange colouration of the integument among sequenced specimens. *Epeolus minimus* from Canada should exhibit reddish orange colouration on at least one of the following: labrum, antenna (scape, pedicel, and F1 in part), and legs. One sequenced specimen (CCDB-28312 A02) from Abbotts Lagoon, California closely resembles the holotypes of *E. arciferus* and *E. pilatei*, and the three specimens were collected at the same time of year (between September and October). This coastal Californian specimen did not barcode differently from sequenced specimens identified as *E. minimus*.

HOST RECORDS: Graenicher (1906) reported *E. minimus* in association with *C. eulophi* Robertson based on detailed observations of a female *Epeolus* that repeatedly examined and entered the nest of a female *Colletes*. No comments were provided with respect to the confidence with which the specimens of either genus were identified to species.

FLORAL RECORDS: Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Chrysothamnus viscidiflorus* (Hook.) Nutt. (Asteraceae), *Grindelia squarrosa* (Pursh) Dunal (Asteraceae), *Helianthus petiolaris* Nutt. (Asteraceae), *Heterotheca villosa* (Pursh) Shinners (Asteraceae), *Mulgedium oblongifolium* (Nutt.) Reveal (Asteraceae), *Potentilla hippiana* Lehm. (Rosaceae), and *Solidago* L. (Asteraceae). Labels of examined voucher specimens further indicate associations with *Chrysopsis* (Nutt.) Elliot (Asteraceae), *Dalea candida* Michx. ex Willd. (Fabaceae), *D. purpurea* Vent., *Melilotus albus* Medik. (Fabaceae), *Malacothrix* DC. (Asteraceae), *Sphaeralcea coccinea* (Nutt.) Rydb. (Malvaceae), *Solidago canadensis* L., and *S. rigida* L.

**Distribution in Canada:** Known to occur in most of Canada except parts of the Atlantic and high Arctic regions (Map 10).

**DNA barcoded material.** Available. BOLD:AAD3554. Specimens examined and sequenced.—CANADA: **Alberta:** Medicine Hat, 13.vi.2007, J. Gibbs and C. Sheffield (1♂, PCYU); Onefour, 23.vii.2010, N. de Silva (1♂, PCYU); **Ontario:** Caledon (Forks of the Credit Provincial Park), 14.vii.2003, J. Grixti (1♂, PCYU); King, 14.vii.2003, A. Gravel (1♀, PCYU); **Saskatchewan:**

Sands Hills (7 km W Piapot), 04.vii.2009, D. Larson (3♂, PCYU); **Yukon:** Takhini River (west dunes 6.8 km NNE Kusawa Lake outlet), 21.vii.2009, L. Mennell (1♂, RSKM).

USA: **California:** Abbotts Lagoon (Point Reyes National Seashore, Marin County), 04.x.2011, J. Powell (1♂, EMEC); **Colorado:** (1♀, PCYU); Near Wolf Creek (Mineral County), 28.vii.2007, J. Gibbs and C. Sheffield (1♀, PCYU); **Idaho:** (1♀, PCYU); Daniels Reservoir (Oneida County), 25.vii.1995, F.D. Parker (1♀, BBSL), 11.vii.1997, F.D. Parker (1♂, BBSL); **Utah:** 5 mi S Long Valley Junction (Kane County), 04.ix.2008, T.L. Griswold (1♀, BBSL).

**Non-barcoded material examined.** CANADA: **Alberta:** Gleichen, 30.vii.1929, G.F. Manson (1♀, CNC), 30.vii.1929, H.L. Seamans (1♀, CNC); Lethbridge, 18.viii.1917, Sladen (1♀, CNC); Medicine Hat, 20.viii.1916, Sladen (4♀, 1♂, CNC), 01.viii.1917, Sladen (2♀, CNC), 15.viii.1917, Sladen (2♂, CNC), 17.viii.1917, Sladen (5♀, 7♂, CNC); Peace River, 12.vii.1932, L.S. Russell (1♀, CNC); **British Columbia:** Clinton (Fish Hatchery on Loon L. Rd.), 11.vii.1969 (1♀, ROM); Kamloops, 13.viii.1948, L.C. Curtis (1♀, CNC); Langford, 14.vii.1960, D. Evans (1♀, CNC), 13.vii.1961, D. Evans (1♀, CNC); Maple Bay (Vancouver Island), 12.vii.1933, J. McDunnough (2♀, CNC); Nicola, 03.viii.1923, E. R. Buckell (1♀, CNC); Salmon Arm, 04.vii.1914, F.W.L. Sladen (1♀, CNC), 26.vi.1925, A.A. Dennys (2♀, CNC), 27.vi.1925, A.A. Dennys (1♀, 1♂, CNC); Vernon, 25.vii.1917, Sladen (3♀, CNC), 28.vii.1920, M.H. Ruhmann (1♀, CNC); **Manitoba:** Aweme, 21.viii.1923, R.M. White (1♂, CNC); Birds Hill, 27.viii.1916, J.B. Wallis (1♀, CNC); Blumenort, 09.vii.1968, T. Harcus (1♂, ROM); Brandon, 11.vii.1916, Sladen (1♂, CNC); Carmen, 30.vii.1968, T. Harcus (1♂, ROM); Delta, 19.vi.1968, T. Harcus (1♂, ROM); La Salle, 10.vii.1973, T.D. Galloway (1♂, DEBU); Riding Mountain National Park of Canada (3 km E Clear Lake), 20.viii.1979, S. and J. Miller (1♀, CNC); Selkirk, 07.viii.1917 (1♀, CNC); Turtle Mountain Forest Reserve (International Peace Garden), 07.viii.1958, J.G. Chillcott (1♂, CNC); Winnipeg, 02.viii.1916, J.B. Wallis (1♀, CNC); **Northwest Territories:** Fort Simpson, 22.vii.1950, D.P. Whillans (1♀, CNC); Fort Smith, 18.viii.1950, J.B. Wallis (2♀, CNC), 27.viii.1950, J.B. Wallis (2♀, CNC); Norman Wells, 13.vii.1949, W.R.M. Mason (1♀, CNC), 23.vii.1949, W.R.M. Mason (1♀, CNC); **Ontario:** Caledon (Forks of the Credit Provincial Park), 15.vii.1968, P. MacKay (1♀, ROM), 15.vii.2002, J. Grixti (1♂, PCYU), 30.vii.2002, J. Grixti (1♀, PCYU); Dyer's Bay, 08-29.vii.1952, D.H. Pengelly (3♀, 2♂, CNC), 13.viii.1953, D.H. Pengelly (1♂, CNC), 30.vii.1953, D.H. Pengelly

(1♂, CNC); King, 14.vii.2003, J. Grixti (1♂, PCYU); Leaside, 07.vii.1959 (1♀, ROM); Norquay Prov. Rec. Area (Portage La Prairie), 10.viii.1970 (1♀, ROM); Rainy River, 05.vii.1960, S.M. Clark (1♀, CNC), 03.viii.1960, S.M. Clark (1♀, CNC); **Quebec:** Mont-Joli, 13.viii.1948, J.R. McGillis (1♂, CNC), 31.vii.1954, J.R. McGillis (1♂, CNC), 01.viii.1954, J.R. McGillis (1♂, CNC); **Saskatchewan:** Christopher Lake, 08-15.vii.1959, A. and J. Brooks (2♀, 1♂, CNC); Elbow, 12.vii.1960, A.R. Brooks (1♂, CNC); Great Sand Hills, 04.vi.1988, M. Polak (1♀, CNC), 11.vii.2010, D. Larson (3♂, PCYU); Harris Res. (10 km S Maple Creek), 15.ix.2004, D. Larson (1♀, PCYU), 16.ix.2004, D. Larson (2♀, PCYU); Heglund Island, 31.vii.2010, D. Larson (1♂, PCYU); Prince Albert, 23.vii.1959, A. and J. Brooks (1♀, 1♂, CNC); Rockglen, 03.viii.1955, C.D. Miller (1♀, CNC); Rutland, 02.viii.1940, A.R. Brooks (1♀, CNC); Sands Hills (7 km W Piapot), 04.vii.2009, D. Larson (3♂, PCYU); **Yukon:** Whitehorse, 04.vii.1948, M.T. Hughes (1♀, CNC), 06.vii.1948, W.R.M. Mason (1♀, CNC).

USA: **California:** 1 mi SE Manila (Humboldt County), 20.viii.1975, J. Powell (1♂, EMEC); Goat Rock State Beach – Sonoma Coast State Park (Sonoma County), 22.viii.1968, M.E. Irwin (2♀, UCR); Hermosa Valley Park, 30.ix.1984, R. Rogers (1♀, UCR); Morro Bay (San Luis Obispo County), 18.viii.1990, J. Powell (1♂, EMEC); Oso Flaco Lake (San Luis Obispo County), 29.vi.1967, M.E. Irwin, T. Cronin, and S. Larisch (1♀, UCR); S Spur Road (Santa Barbara County), 25.vi.2005, G.R. Ballmer (1♂, UCR); San Pedro Naval fuel reserve site (Los Angeles County), 28.iii.1995, R. Rogers and R. Mattoni (1♂, UCR); **Florida:** Lee County, 10.xi.1983, L. Packer (1♀, PCYU); **Idaho:** Ketchum (Blaine County), 24.vi.2007, J. Gibbs and C. Sheffield (1♀, PCYU); **Illinois:** Argonne National Laboratory (DuPage County), 11.vii.1967, J. Wagner (1♂, FMNH); **Montana:** 17 km N. Billings (Yellowstone County), C.D. Michener (1♀, KUNHM); **Oregon:** Tumalo Reservoir, 23.vi.1954, G.F. Knowlton (1♂, KUNHM); **South Dakota:** Badlands National Park (Pennington County), 19.vi.2012, S.W. Droege (1♀, BIML).

**11. *Epeolus olympiellus* Cockerell, 1904 (Figures 1b, 2b, 3c, 14b, 15c, 16b, 18b, 19, 20; Plate 1, Figure K; Plate 2, Figure K; Plate 3, Figure K; Map 11)**

*Epeolus olympiellus* Cockerell, 1904. Ann. Mag. Nat. Hist. 13: 41 (♂).
**Primary type specimen.** Holotype ♂ (USNM, catalog number: 534051). **Collection information.** USA: Washington: Olympia, 02.vii.1896, T. Kincaid.

*Epeolus tristicolor* Viereck, 1905. Can. Entomol. 37: 280 (♀), **new synonymy**
**Primary type specimen.** Holotype ♀ (ANSP, catalog number: 10123). **Collection information.** CANADA: British Columbia: Vancouver.

*Epeolus humillimus* Cockerell, 1918. Ann. Mag. Nat. Hist. (9) 1: 160 (♂), **new synonymy**
**Primary type specimen.** Holotype ♂ (USNM, catalog number: 534047). **Collection information.** USA: Washington: Pullman, 02.viii.1908, W.M. Mann.

*Epeolus rufomaculatus* Cockerell and Sandhouse, 1924. Proc. Calif. Acad. Sci. (4) 13: 314 (♀), **new synonymy**
**Primary type specimen.** Holotype ♀ (CAS, catalog number: 01609). **Collection information.** USA: Utah: Logan, 14.vii.1922, E.P. Van Duzee.

*Epeolus rubrostictus* Cockerell and Sandhouse, 1924. Proc. Calif. Acad. Sci. (4) 13: 318 (♀), **new synonymy**
**Primary type specimen.** Holotype ♀ (CAS, catalog number: 01613). **Collection information.** CANADA: British Columbia: Nanaimo (Nanaimo Biological Station), 24.vi.1920, E.P. Van Duzee.

**Diagnosis.** Among Canadian species, *Epeolus olympiellus* most closely resembles *E. minimus*. In *E. olympiellus*, T3 and T4 are with fasciae that may be entirely broken or greatly narrowed laterally, whereas in *E. minimus* T3 and T4 are with fasciae that are complete or only broken medially. The labrum, antenna, and legs of *E. olympiellus* are extensively dark and lack the bright reddish orange colouration typical of Canadian *E. minimus*. For an extensive list of similarities to *E. minimus* and comments with regard to separation from other species in Canada, see diagnosis for *E. minimus*.

**Redescription.** MALE: Length 7.5 mm; head length 2.2 mm; head width 2.9 mm; fore wing length 6.0 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, and legs. Mandible with apex darker than all but extreme base. Preapical tooth as dark as mandibular apex (difficult to see in the *E. olympiellus* holotype; described from the *E. humillimus* holotype). Antennae, except left scape and pedicel, missing in the *E. olympiellus* holotype. Flagellum of most similar sequenced specimen brown and (except F1) faintly lighter than dark brown scape and pedicel, generally due to extensive pilosity on flagellum. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs, except tarsi, more extensively brown or black than reddish orange.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron with upper half densely hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum uninterrupted except for median bare patch on apical half, uniformly pale yellow. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2–T5 with fasciae interrupted medially and narrowed before becoming somewhat broader laterally, and T2 with fascia with anterolateral extensions of sparser tomentum. S4 and S5 with long silvery to coppery subapical hairs, which individually are often darker apically.

*Surface sculpture.* Punctures dense. Labrum with areas of sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate spot present lateral to lateral ocellus (larger and shinier in the *E. humillimus* holotype than in the *E. olympiellus* holotype). Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i<1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labrum with pair of small subapical denticles preceded by small discreet ridges. Frontal keel present. Scape with greatest length 1.6 × greatest width. F2 (missing in the *E. olympiellus* holotype) short in the *E. humullimus* holotype, not noticeably longer than wide (L/W ratio = 1.1). Preoccipital ridge not joining hypostomal carina, from which it is separated by 1.5 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.40) and tip not extending much

beyond midlength of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing (on each side) with second submarginal crossvein incomplete. Pygidial plate mostly hidden in the *E. olympiellus* holotype, but apically rounded, with large deep punctures apically. Punctures sparser basally with the interspaces shining in non-type specimens.

FEMALE: Description as for male except for usual secondary sexual characters and as follows: F2 noticeably longer than wide (L/W ratio = 1.3); T5 with two patches of pale tomentum bordering and separate from pseudopygidial area present only in female; T5 with pseudopygidial area lunate, its apex at least twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S4 and S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 1/3 MOD); Pygidial plate apically truncate.

**Male hidden sterna.** Plate 2, Figure K.

**Male genitalia.** Plate 3, Figure K.

**Discussion.** *Epeolus olympiellus* is a highly variable species that has been the subject of much taxonomic confusion. Cockerell (1904) believed it to be closely related to *E. interruptus*, but it is much more similar to *E. minimus*.

A female specimen from Vancouver, British Columbia, Canada was described as a new species (*E. tristicolor*) by Viereck (1905), and was said to be related to *E. autumnalis* (a very different species), to which it was said to differ in colour, size, and structure. Although Viereck (1905) acknowledged *E. olympiellus* as a distinct species, no comparisons were made between it and *E. tristicolor*. The holotype of *E. tristicolor* is not as robust (head length 1.9 mm; head width 2.6 mm) as that of *E. olympiellus*, but the two specimens are equally long, partly because T6 of the *E. olympiellus* type specimen is almost completely retracted. Much of the pubescence is rubbed off in the *E. tristicolor* holotype (Figure 19a), but the pattern of the tomentum on the mesosoma and metasoma that is visible is essentially the same.

Cockerell (1918) described a male specimen from Pullman, Washington, USA under the name *E. humillimus*, which was distinguished from *E. olympiellus* by its smaller size, partially ferruginous labrum (light brown markings laterally), and (supposedly) lighter tegula. Since its original description, the metasoma of the *E. humillimus* holotype has been lost, but otherwise the specimen is most similar in size to the *E. tristicolor* holotype (Figure 19a, 19b). In terms of body size, the type specimens of *E. humillimus*, *E. olympiellus*, and *E. tristicolor* fall within the range of variation of sequenced specimens (Figure 19c, 19d, 19g).

In Cockerell and Sandhouse (1924), this species was described again under two names (*E. rubrostictus* and *E. rufomaculatus*). *Epeolus rubrostictus* was said to resemble *E. humillimus*, but otherwise no comparisons were made to any of the abovementioned "species". In the holotype of *E. rubrostictus*, the fasciae of T3 and T4 are medially separated and greatly narrowed, respectively, and broken laterally (Figure 19e). Although the apical fasciae of T1–T4 are separated medially in most sequenced specimens, those of T3 and T4 may be laterally complete, narrowed to varying degrees, or entirely broken. Sequenced specimens from the same localities exhibit variation in T3 and T4 pubescence, and were assigned the same BIN. Even in the same specimen (e.g. CCDB-22015 F05), the fascia may be broken on one side and greatly narrowed on the other. By contrast, I have not seen any specimens of the related *E. minimus* in which the metasomal fasciae are broken laterally. The holotype of *E. rubrostictus* (a female) is only slightly longer (7.9 mm) than that of *E. olympiellus* (a male).

*Epeolus rufomaculatus* was identified as distinct based on the occurrence of two ferruginous maculations in the female on either side of the pseudopygidial area of T5 (Figure 20a). In the holotype (Figure 19f), these were clearly once covered in pale pubescence, but most of this has been rubbed off. In *E. rubrostictus* and *E. tristicolor*, the integument of these equivalent two areas of T5 is mostly obscured by pubescence, but is clearly black. Specimens with either black or red integument underlying these spots were sequenced (Figure 20b, 20c), and all specimens were assigned the same BIN. One female specimen (Figure 19g) resembles both the *E. olympiellus* holotype (Figure 19h), in that the second submarginal crossvein of the right fore wing is incomplete (the left fore wing has three submarginal cells), and the *E. rufomaculatus* holotype, in that T5 is with two large ferruginous maculations. There is continuous variation in the size of the red spot from absent to nearly as large as the spot of pale tomentum obscuring it. I have, however, not seen any specimens of *E. minimus* with ferruginous

maculations on T5, so the feature, when present, seems to be unique to females of *E. olympiellus*. The type locality of *E. rufomaculatus* is Logan, Utah, which falls well within the range of sequenced specimens (from Mendocino County, California in the south to Mineral County, Colorado in the east). The holotype of *E. rufomaculatus* is equal in size to that of *E. olympiellus* (length 7.5 mm; head length 2.2 mm; head width 2.9 mm).

HOST RECORDS: Sampling a small island off of Vancouver Island, British Columbia, Canada yielded a long series of *E. olympiellus*, and the only (potential host) *Colletes* species caught in the same traps was *C. hyalinus* Provancher (C. Sheffield, personal communication, 2017).

FLORAL RECORDS: The label of one examined voucher specimen indicates a floral association with *Ericameria* Nutt. (Asteraceae).

**Distribution in Canada:** British Columbia, west of the Rocky Mountains (Map 11).

**DNA barcoded material.** Available. BOLD:AAC6215. Specimens examined and sequenced.—USA: **California:** (1♀, PCYU); Hwy 20 (Mendocino County), 05.vii.2007, J. Gibbs and C. Sheffield (1♀, 4♂, PCYU); **Colorado:** Near Wolf Creek (Mineral County), 28.vii.2007, J. Gibbs and C. Sheffield (2♀, 1♂, PCYU); **Idaho:** Ketchum (Blaine County), 24.vi.2007, J. Gibbs and C. Sheffield (2♀, PCYU); **Oregon:** Hwy 26 (Crook County), 28.vi.2007, J. Gibbs and C. Sheffield (1♀, PCYU); Hwy 26 (Wheeler County), 28.vi.2007, J. Gibbs and C. Sheffield (1♀, PCYU); Hwy 97 (Klamath County), 02.vii.2007, J. Gibbs and C. Sheffield (1♂, PCYU); **Washington:** 25 km W Clarkston (Garfield County), 29.v.2007, J. Gibbs and C. Sheffield (1♂, PCYU); **Wyoming:** 25 km ESE Eden (near Killpecker Sand Dunes, Sweetwater County), 24.vii.2012, M.C. Orr (1♀, BBSL); Pacific Creek Road (Teton County), 13.viii.2013, A. Payne (1♀, AMNH).

**Non-barcoded material examined.** CANADA: **British Columbia:** Comox, 08.vii.1933, J. McDunnough (1♂, CNC), 05.vii.1933, J. McDunnough (1♂, CNC); Langford, 13.vii.1961, D. Evans (1♀, CNC), 19.vii.1960 (1♀, CNC); Oliver, 29.viii.1953, D.F. Hardwick (1♀, CNC); Penticton, 23.viii.1920, W. Downes (1♀, 1♂, CNC); The District of Saanich, 17.vi.1926, W.

Downes (1♀, CNC); Victoria, 02.vii.1920, W. Downes (1♂, CNC), 07.vii.1923, K.F. Auden (1♂, CNC).

USA: **California:** Hwy 20 (Mendocino County), 05.vii.2007, J. Gibbs and C. Sheffield (3♀, 2♂, PCYU); Sagehen Creek Field Station (Nevada County), 22-24.vi.1985, D.C. Darling (1♀, PCYU); **Colorado:** Near Wolf Creek (Mineral County), 28.vii.2007, J. Gibbs and C. Sheffield (3♀, 4♂, PCYU); **Idaho:** Ketchum (Blaine County), 24.vi.2007, J. Gibbs and C. Sheffield (6♀, PCYU); **Oregon:** Hwy 26 (Wheeler County), 28.vi.2007, J. Gibbs and C. Sheffield (1♀, PCYU); Lane County, 01.vii.2007, J. Gibbs and C. Sheffield (1♂, PCYU).

**12. *Epeolus pusillus* Cresson, 1864 (Figures 3d, 9d, 13a; Plate 1, Figure L; Plate 2, Figure L; Plate 3, Figure L; Map 12)**

*Epeolus pusillus* Cresson, 1864a. Proc. Entomol. Soc. Phil. 2: 398 (♀).
**Primary type specimen.** Holotype ♀ (ANSP, catalog number: 2228). **Collection information.** USA: Massachusetts: no specific locality given, F.G. Sanborn.

**Diagnosis.** Among Canadian species, *E. pusillus* most closely resembles *E. scutellaris*. Both species exhibit the following similarities: axilla large and robust, its tip attaining or surpassing line of pale tomentum marking posterior margin of mesoscutellum, and its lateral margin arcuate; T1 with discal patch very wide; and metasomal fasciae rather thin. Differences are as follows: in *E. pusillus*, mesopleuron of male entirely obscured by white tomentum; at least mesoscutellum entirely black (entirely black to entirely ferruginous in *E. scutellaris*); and T5 with pseudopygidial area of female narrower (apex <2 × medial length) than in *E. scutellaris* (apex ≥2 × medial length). In addition to the diagnostic differences included in the key are the following: in contrast to *E. scutellaris*, paramedian band of *E. pusillus* may be quite long, attaining or surpassing 3/5 length of entire mesoscutum; and in *E. pusillus*, fascia of T2 always with lobe-like anterolateral extensions of tomentum, whereas in *E. scutellaris* such extensions may be entirely absent.

**Redescription.** FEMALE: Length 6.9 mm; head length 1.8 mm; head width 2.4 mm; fore wing length 5.0 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, legs, pygidial plate, and metasomal sterna. Mandible with apex darker than all but extreme base. Preapical tooth faintly lighter than mandibular apex (difficult to see in holotype; described from non-type specimens). Antenna brown except scape, pedicel, and F1 extensively orange. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron mostly bare (with tomentum rubbed off) in holotype, but tomentum dense in non-type specimens, except for two almost entirely bare patches (one beneath base of fore wing (hypoepimeral area), a larger circular patch occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally. T1–T3 with apical fasciae partly rubbed off medially and laterally in holotype, but apical fasciae complete (basal fascia of T1 also) and narrowed or narrowly interrupted medially, and T2 with fascia with anterolateral extensions of tomentum in non-type specimens. T4 with fascia complete medially and narrowed laterally. T5 with large, continuous patch of pale tomentum bordering and contacting pseudopygidial area. T5 with pseudopygidial area lunate, its apex less than twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger punctures than clypeus, but punctures of both more or less equally dense (i<1d). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth obtuse. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel present. Scape with greatest length 1.9 × greatest width. F2

noticeably longer than wide (L/W ratio = 1.7). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5–2 MOD at its terminal (difficult to see in holotype; described from non-type specimens). Mesoscutellum weakly bigibbous. Axilla large, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.52) and tip extending well beyond midlength of mesoscutellum but not attaining apex; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.2); mesopleuron entirely obscured by white tomentum; S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep, well-separated punctures, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure L.

**Male genitalia.** Plate 3, Figure L.

**Discussion.** This species exhibits sexual dimorphism in the pubescence of the mesopleuron, which in males is entirely obscured by white tomentum whereas in females there is a sparsely hairy circle occupying much of the ventrolateral half of the mesopleuron, as well as a sparsely hairy patch beneath the base of the fore wing (hypoepimeral area). With regard to the axilla and mesoscutellum, integument colouration is remarkably consistent among specimens. The mesoscutellum is all black, and typically the axilla is black except along the lateral edge, where it is ferruginous. I have come across only a few specimens in which the axilla is all black. Unless rubbed off, the apical fascia of T2 is with anterolateral extensions of tomentum. Although the pseudopygidial area of the female T5 is proportionally longer in this species compared to that of the similar *E. scutellaris*, it is still in the shape of a lunule.

HOST RECORDS: A known *Colletes* host of *E. pusillus* is *C. compactus compactus* Cresson, an association confirmed by Rozen and Favreau (1968).

FLORAL RECORDS: Robertson (1929) reported *E. pusillus* on *Bidens* L. (Asteraceae), *Boltonia* L'Hér. (Asteraceae), *Coreopsis* L. (Asteraceae), *Helianthus* L. (Asteraceae), and *Polygonum* L. (Polygonaceae). Mitchell (1962) indicated additional associations with *Aster* (now

*Symphyotrichum* Nees) (Asteraceae), *Erigeron* L. (Asteraceae), *Eupatorium* L. (Asteraceae), *Haplopappus* Cass. (Asteraceae), *Helenium* L. (Asteraceae), *Melilotus* Mill. (Fabaceae), and *Solidago* L. (Asteraceae). Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Achillea millefolium* L. (Asteraceae), *Erigeron strigosus* Muhl. ex Willd., *Ilex glabra* (L.) A. Gray (Aquifoliaceae), *Limonium carolinianum* (Walter) Britton (Plumbaginaceae), *Ocimum basilicum* L. (Lamiaceae), *Pityopsis falcata* (Pursh) Nutt. (Asteraceae), *P. graminifolia* (Michx.) Nutt., *Pluchea* Cass. (Asteraceae), *Solidago nemoralis* Aiton, and *S. sempervirens* L. Labels of examined voucher specimens further indicate associations with *Melilotus albus* Medik., *Solidago altissima* L., *S. bicolor* L., and *Symphyotrichum ericoides* (L.).

**Distribution in Canada:** Central Canada (Map 12).

**DNA barcoded material.** Available. BOLD:AAX7180. Specimens examined and sequenced.—CANADA: **Ontario:** King, 28.viii.2002, V. Kushnir (1♂, PCYU).

USA: **Maryland:** Jug Bay Wetlands Sanctuary (Anne Arundel County), 15.ix.2007, S.W. Droege (1♂, BIML); **Utah:** 4.17 mi SE Wig Mountain (Toole County), 26.ix.2005, T.L. Griswold (1♀, BBSL); Beef Basin Rd (N Cottonwood Creek, San Juan County), 03.x.2014, M.C. Orr (1♀, BBSL).

**Non-barcoded material examined.** CANADA: **Ontario:** Caledon, 04.ix.2003, A. Gravel (1♀, PCYU); Caledon (Forks of the Credit Provincial Park), 12.viii.1968, P. MacKay (1♂, ROM), 20.viii.1968, P. MacKay (2♀, ROM), 25.vii.1968, P. MacKay (1♂, ROM), 27.viii.1968, P. MacKay (3♀, ROM), 21.viii.1969, P. MacKay (1♂, PCYU), 26.viii.1969, P. MacKay (1♀, 1♂, ROM), 27.viii.2002, J. Grixti (1♂, PCYU); Grand Bend, 20.viii.1936, A.A. Wood (1♂, CNC); King, 23.viii.2000, J. Grixti (3♂, PCYU), 14.viii.2001, M. Somers (1♂, PCYU), 21.viii.2001, M. Somers (1♂, PCYU), 29.viii.2001, M. Somers (1♂, PCYU), 23.vii.2002, J. Grixti (3♂, PCYU), 17.viii.2002, J. Grixti (1♂, PCYU), 23.viii.2002, V. Kushnir (1♂, PCYU), 28.viii.2002, J. Grixti (1♂, PCYU), 28.viii.2002, V. Kushnir (1♀, 2♂, PCYU), 14.ix.2002, J. Grixti (1♀, PCYU), 06.ix.2003, A. Gravel (1♂, PCYU), 06.ix.2003, J. Grixti (2♀, 1♂, PCYU); Ottawa, 25.viii.1954, W.R.M. Mason (1♂, CNC); Vankleek Hill, 01.ix.1974, J.T. Huber (1♀, DEBU); Windsor

(Ojibway Prairie), 22.ix.2001, S.M. Paiero (1♀, DEBU); **Quebec:** Buckingham, Gatineau, 23.ix.1965, B.V. Peterson (1♀, CNC).

USA: **Florida:** Alachua County, 06.v.1955, R.A. Morse (1♂, AMNH); **Illinois:** Olive Branch, 01.ix.1909, Gerhard (1♀, FMNH); **Indiana:** Gibson County, 08.ix.1956 (1♂, USNM); **Maryland:** Anne Arundel County, 20.ix.2004, R. Andrus (1♂, BIML); Assateague Island (Worcester County), 19.ix.2006, S.W. Droege (1♀, 5♂, BIML), 20.ix.2006, S.W. Droege (2♂, BIML); Jug Bay Wetlands Sanctuary (Anne Arundel County), 15.ix.2007, S.W. Droege (1♀, BIML); **Massachusetts:** Suffolk County, 14-15.ix.2010, J. Rykken (2♀, 4♂, BIML); **Mississippi:** Hattiesburg (Forrest County), 08.x.1944, C.D. Michener (1♂, AMNH); **Montana:** Ashland (Rosebud County), 11.viii.1970, D.R. Miller (1♀, USNM); **New Jersey:** Jamesburg, 20.ix.1909, W.T. Davis (1♀, AMNH); **New York:** Lewisboro (Westchester County), 17.ix.1967, M. Favreau (1♀, AMNH), 04.x.1967, M. Favreau (1♀, AMNH); **Oklahoma:** 15 mi S Altus (Jackson County), 02.iv.1979, R.J. McGinley (1♂, USNM); **South Carolina:** Carolina Sandhills National Wildlife Refuge (Chesterfield County), 26.ix.2007, S.W. Droege (1♀, BIML); Hobcaw Barony (5 km E Georgetown, Georgetown County), 11-17.ix.2007, S.M. Paiero (1♂, DEBU).

**13. *Epeolus scutellaris* Say, 1824 (Figures 3e, 13b; Plate 1, Figure M; Plate 2, Figure M; Plate 3, Figure M; Map 13)**

*Epeolus scutellaris* Say, 1824. In Keating, Narr. Long's 2nd Exped., v. 2: 355 (♀), **new neotype designation**

**Primary type specimen.** Neotype ♀ (AMNH). **Collection information.** USA: New York: Keene Valley (Essex County), 12.viii.1917, H. Notman.

*Epeolus vernoniae* Cockerell, 1907. Entomologist 40: 136 (♂).

**Primary type specimen.** Holotype ♂ (AMNH). **Collection information.** USA: Virginia: Falls Church, 04.ix.????, N. Banks.

**Diagnosis.** This species most closely resembles *E. pusillus*, but can be easily distinguished as follows: mesopleuron of male not entirely obscured by white tomentum (unlike in *E. pusillus*), but with sparsely hairy circle occupying much of ventrolateral half; and T5 with pseudopygidial

area of female wider (apex ≥2 × medial length) than in *E. pusillus* (apex <2 × medial length). For a comprehensive list of secondary distinguishing features and similarities to *E. pusillus*, see diagnosis for *E. pusillus*.

**Redescription.** FEMALE: Length 8.2 mm; head length 2.1 mm; head width 3.0 mm; fore wing length 6.7 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, and legs. Mandible with apex darker than all but extreme base. Preapical tooth faintly lighter than mandibular apex (difficult to see in the *E. scutellaris* neotype; described from non-type specimens). Antenna brown except scape, pedicel, and F1 extensively orange. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum with orange spot anterolaterally between pronotal lobe and tegula. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron mostly bare, but tomentum moderately dense ventrally as well as between two almost entirely bare circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae at most only narrowly joined laterally (not joined in the *E. scutellaris* neotype and multiple non-type specimens). T1 with basal fascia interrupted medially, T1–T4 with apical fasciae complete and somewhat broader laterally. T5 with large, continuous patch of pale tomentum bordering but not contacting pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 1/3 MOD.

*Surface sculpture.* Punctures dense. Labrum with sparser punctures (i=1–2d) than clypeus (i<1d). Impunctate spot lateral to lateral ocellus absent in the *E. scutellaris* neotype, but dull/textured spot present in non-type specimens. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally

(i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth blunt and obtuse. Labral apex with pair of small denticles preceded by carinae. Frontal keel present. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by less than 1 MOD at its terminal (difficult to see in the *E. scutellaris* neotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla large, its lateral margin more than half as long as mesoscutellar width (L/W ratio = 0.62) and tip attaining apex of horizontal dorsal portion of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, not noticeably longer than wide (L/W ratio = 1.1); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate with large deep punctures closely clustered basally and sparser apically, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure M.

**Male genitalia.** Plate 3, Figure M.

**Discussion.** *Epeolus scutellaris* exhibits some variation in the size of the axilla relative to the mesoscutellum, and in this species the axilla may extend farther posteriorly than in any other species of *Epeolus* in Canada. At least the axilla is ferruginous to some degree, whereas the mesoscutellum may range from entirely black to entirely ferruginous. Although in examined specimens from Canada the fascia of T2 is commonly without lobe-like anterolateral extensions of tomentum, specimens from Western North America typically possess them.

The whereabouts of the primary type of *E. scutellaris* is unknown, but in all likelihood it has been destroyed, along with much of Thomas Say's entomological collection (LeConte 1859:v–vi, xix (footnote)). Mawdsley (1993) lists 71 surviving insect specimens housed in the MCZ of 56 species described by Say, upon which Say's original descriptions are probably based,

that have yet to be recognized as primary types. Of the four specimens of Hymenoptera listed, all are Ichneumonidae. Specimens identified as *E. scutellaris* in the MCZ were only recently collected (in 2010). I have not been able to locate any *Epeolus* specimens collected or identified by Say in any other entomological institution, despite extensive searches.

Similar to *E. scutellaris* is at least one undescribed species from Florida with a unique barcode sequence, and potentially another (also from Florida) yet to be sequenced. In an NJ tree of COI sequence data, *E. scutellaris* is grouped closest with the undescribed sequenced species from Florida. Before formally describing any additional similar-looking species, it is sensible to first have a neotype designated for *E. scutellaris* for reference to ensure proper name use is standardized.

*Epeolus scutellaris* was originally described (♀ only) as exhibiting the following features typically associated with the species: the mandible, antenna (excluding F2–F12), axilla, mesoscutellum, and legs are ferruginous; the integument of the body is otherwise black and densely punctate; the axilla is dilated; and the metasomal terga are with pale yellow fasciae. In the original description, this species is said to inhabit the middle states, presumably referring to the Middle Atlantic States. Herein, I designate a neotype female from Keene Valley in Essex County, New York, which falls within Say's (1824) indicated range for this species and matches the original description. The redescription of *E. scutellaris* provided here is based on this neotype specimen.

Mitchell (1962) synonymized *E. vernoniae* under *E. scutellaris*. I have examined the male holotype specimen of *E. vernoniae,* and agree with Mitchell's treatment. The neotype of *E. scutellaris* is the property of the AMNH, the same institution where the holotype of *E. vernoniae* is housed, which should make future comparisons of the two specimens more convenient for researchers.

HOST RECORDS: An inferred *Colletes* host of *E. scutellaris*, based on frequent co-occurrence, is *C. simulans armatus* Patton (Ascher *et al*. 2014), although this association has not yet been confirmed.

FLORAL RECORDS: Mitchell (1962) indicated floral associations with *Baccharis* L. (Asteraceae), *Bidens* L. (Asteraceae), and *Solidago* L. (Asteraceae). Collection records on Discover Life (Ascher and Pickering 2016) indicate the following associations: *Euthamia graminifolia* (L.) Nutt. (Asteraceae), *Pityopsis falcata* (Pursh) Nutt. (Asteraceae), *Pluchea*

*odorata* (L.) Cass. (Asteraceae), *Solidago nemoralis* Aiton, *S. rugosa* Mill., *S. sempervirens* L., and *Symphyotrichum* Nees (Asteraceae). Labels of examined voucher specimens further indicate associations with *Allium tricoccum* Aiton (Amaryllidaceae), *Cirsium arvense* (L.) Scop. (Asteraceae), *Melilotus albus* Medik. (Fabaceae), *Solidago altissima* L., *S. bicolor* L., and *Symphyotrichum lateriflorum* (L.) Á. Löve and D. Löve.

**Distribution in Canada:** Atlantic and Central Canada (Map 13).

**DNA barcoded material.** Available. BOLD:AAG5250. Specimens examined and sequenced.—CANADA: **Nova Scotia:** Pereau (Kings County), 10.ix.2002, C. Sheffield (1♀, RSKM); **Ontario:** Cumberland (Ottawa: Baseline Rd & Canaan Rd), 14.viii.2016, T.M. Onuferko (1♂, PCYU); Grand Bend (Lambton County), 10.ix.2008, A. Taylor (1♀, PCYU).

USA: **Idaho:** Saint Anthony (Fremont County), 09.viii.2013, A. Payne (2♂, AMNH).

**Non-barcoded material examined.** CANADA: **New Brunswick:** Kouchibouguac, 02.viii.1978, D.B. Lyons (1♂, CNC); Saint Andrews, 11.viii.1957, G.E. Shewell (1♀, CNC); **Nova Scotia:** Avonport (Kings County), 27-28.viii.2000, C. Sheffield (2♀, PCYU), 14.ix.2000, C. Sheffield (1♀, RSKM); Brier Island (Digby County), 13.viii.2002, C. Sheffield (1♀, 1♂, PCYU); Evang. Beach (Kings County), 10.ix.2000, C. Sheffield (1♀, RSKM); Kemptown (Colchester County), 04.viii.1999, J. Ogden (1♀, PCYU); Kings County, 15.viii.1931, C.E. Atwood (3♂, CNC); Melford, 25.viii.1985, L. Packer (1♂, PCYU); Pereau beach (Kings County), 29.viii.2005, C. Sheffield and S. Westby (1♀, PCYU), 10.ix.2002, C. Sheffield (1♀, PCYU); River Denys Mtn Rd, 24.viii.1985, L. Packer (1♂, PCYU), 01.ix.1985, L. Packer (1♂, PCYU); Valley Mills (Cape Breton Island), 08.ix.1985, L. Packer (1♀, PCYU); Weymouth, 3-10.viii.1900 (1♀, 1♂, CNC); Wreck Cove (Cape Breton Island), 30.viii.1981, L. Packer (1♀, PCYU); **Ontario:** Albion Hills Conservation Area, 21.viii.2012, S. Dumesh (1♂, PCYU);
Bobcaygeon (Emily Creek, Peterborough County), 18.viii.1975, F. Quan (1♂, ROM); Brighton, 02.ix.1954, J.C. Martin (1♂, CNC); Burketon, 30.viii.1954, C.D. Miller (1♀, CNC); Caledon, 02.ix.2003, J. Grixti (1♂, PCYU); Caledon (Forks of the Credit Provincial Park), 08.viii.1968, P. MacKay (1♂, ROM), 12.viii.1968, P. MacKay (1♂, ROM), 18.viii.1969, P. MacKay (1♀, PCYU), 18.viii.1969, P. MacKay (1♀, ROM), 21.viii.1969, P. MacKay (1♀,

ROM), 27.viii.1968, P. MacKay (1♀, PCYU), 27.viii.1968, P. MacKay (2♀, 1♂, ROM), 08.ix.2003, J. Grixti (1♂, PCYU), 13.ix.2002, J. Grixti (1♀, PCYU), 13.viii.2003, A.I. Gravel (1♂, PCYU), 18.ix.2003, J. Grixti (2♀, PCYU); Conc. 11 near Hume Rd (Puslinch), 10.ix.2002, P. Hebert (1♀, PCYU); Dunnville, 03.viii.1954, C.D. Miller (1♂, CNC); King (1♂, PCYU), 06.ix.2003, J. Grixti (2♀, 1♂, PCYU), 08.viii.2001, M. Somers (2♂, PCYU), 12.ix.2000, J. Grixti (1♀, PCYU), 23.vii.2002, J. Grixti (1♂, PCYU), 23.viii.2000, V. Kushnir (1♂, PCYU), 23.viii.2002, V. Kushnir (1♂, PCYU), 28.viii.2002, J. Grixti (2♀, 2♂, PCYU), 28.viii.2002, V. Kushnir (3♀, 1♂, PCYU), 21.viii.2001, M. Somers (4♂, PCYU), 29.viii.2001, M. Somers (1♂, PCYU); Lake of the Woods (Harris Hill), 3-4.viii.1960, Kelton and Whitney (1♂, CNC); Manester Tract (St. Williams), 01.ix.1992, P.J. Carson (1♂, PCYU); Normandale, 04.ix.1954, C.D. Miller (1♀, CNC); Orono, 03.ix.1925, N.K. Bigelow (1♀, ROM); Ottawa, 25.viii.1954, W.R.M. Mason (1♀, 1♂, CNC); Peel Reg. Mun Hart House Farm (near Cheltenham), 19.ix.1992, D.C. Darling (1♂, ROM); Queen's University Biological Station (Main HQ), 02.ix.2001, A. Zayed (4♀, PCYU); Spencerville, 20.viii.1938, G.H. Hammond (1♀, CNC); Thousand Islands National Park, 05.ix.1976, Reid (1♀, CNC); Toronto (York University Campus), 31.viii.2006, E. Willis (1♀, PCYU); **Quebec:** 8 km SE Rigaud, 08.ix.1985, J.S. Noyes (1♀, CNC); Fort-Coulonge, 20-23.viii.1917, J.I. Beaulne (2♂, CNC); Hull (Gatineau), 13.ix.1965 (1♀, CNC); Mont Ste. Marie, 20.ix.1965, J.R. Vockeroth (1♀, CNC).

USA: **Maine:** Blue Hill, 22.viii.2012, E. Venturini (1♂, BIML); Columbia Falls, 21.viii.2013, (1♀, BIML); Jonesboro, 20.viii.2013, E. Venturini (1♀, BIML); **Maryland:** Assateague Island (Worcester County), 19.ix.2006, S.W. Droege (4♂, BIML); **Michigan:** Alger County, 1-2.ix.2011, J. Gulbransen and C. Heyd (1♀, BIML); **New Jersey:** Montvale (Bergen County), 12.viii.1949, B.L. and J.G. Rozen (1♂, AMNH); **North Carolina:** Black Mountains (1♂, AMNH); **Vermont:** Chittenden (Rutland County), 15.viii.1916 (1♀, 2♂, AMNH); **Wisconsin:** Friendship (Adams County), vi.1965, O. Perk (1♀, FMNH).

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**Figures**

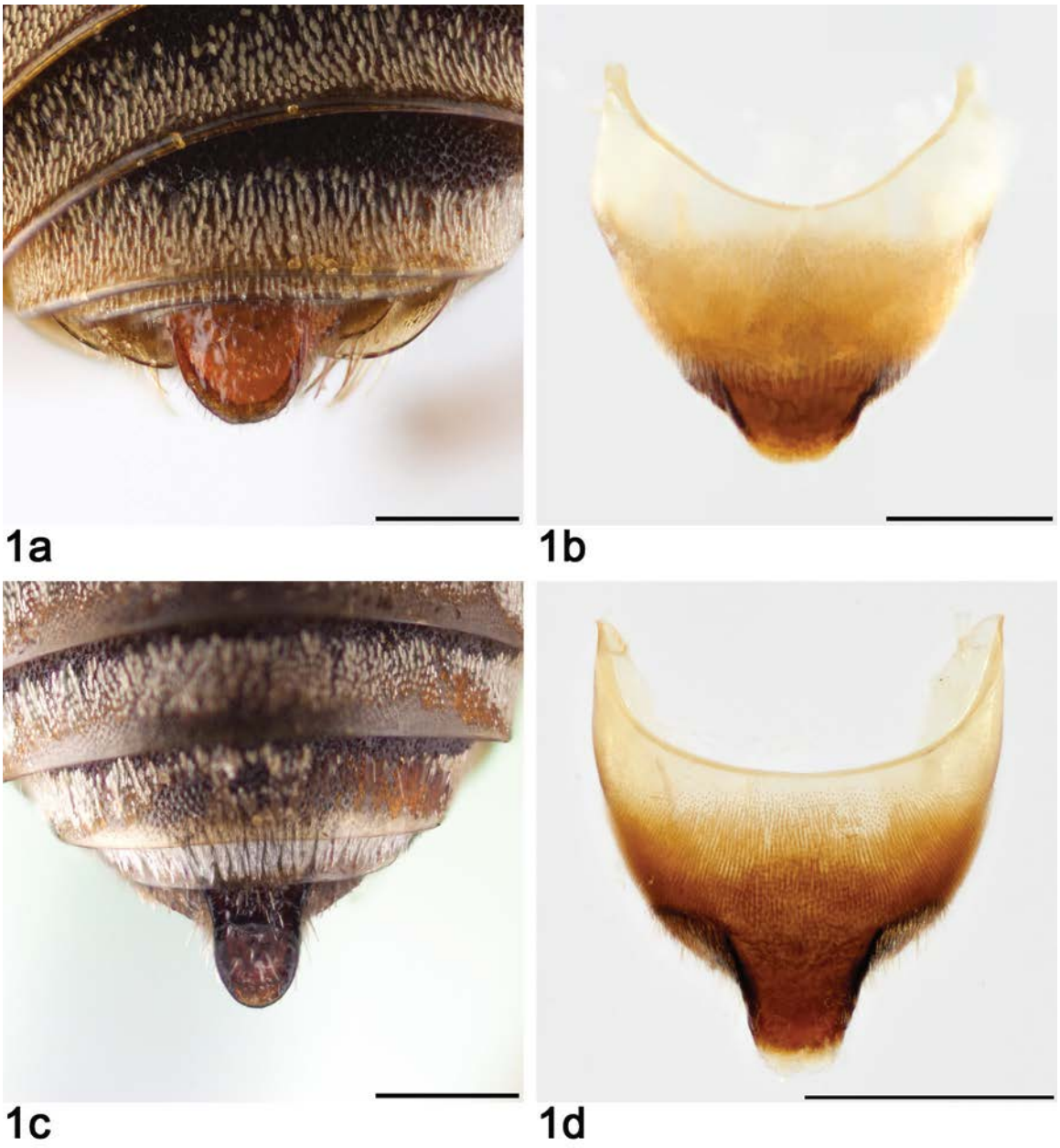



**Figure 1.** Morphological differences in the T7 of male *Epeolus* (a, b) and *Triepeolus* (c, d). Pygidial plate is shown for pinned specimens of a) *E. ainsliei* and c) *T. pectoralis* (Scale bars = 0.5 mm) (dorsal view). Pygidial plate is shown entirely removed and cleared in KOH for specimens of b) *E. olympiellus* (Scale bar = 0.5 mm) and d) *T. lunatus* (Scale bar = 1 mm) (dorsal view).


**Figure 2.** Morphological differences in the terminalia of female *Epeolus* (a, b) and *Triepeolus* (c, d). S6 with exposed lateral processes is shown for pinned specimens of a) *E. ainsliei* bearing setae modified into pointed denticles and c) *T. pectoralis* bearing coarse spine-like setae (Scale bars = 0.5 mm) (dorsal view). S6 is shown entirely removed and cleared in KOH for specimens of b) *E. olympiellus* and d) *T. lunatus* (Scale bars = 1 mm) (dorsal view).

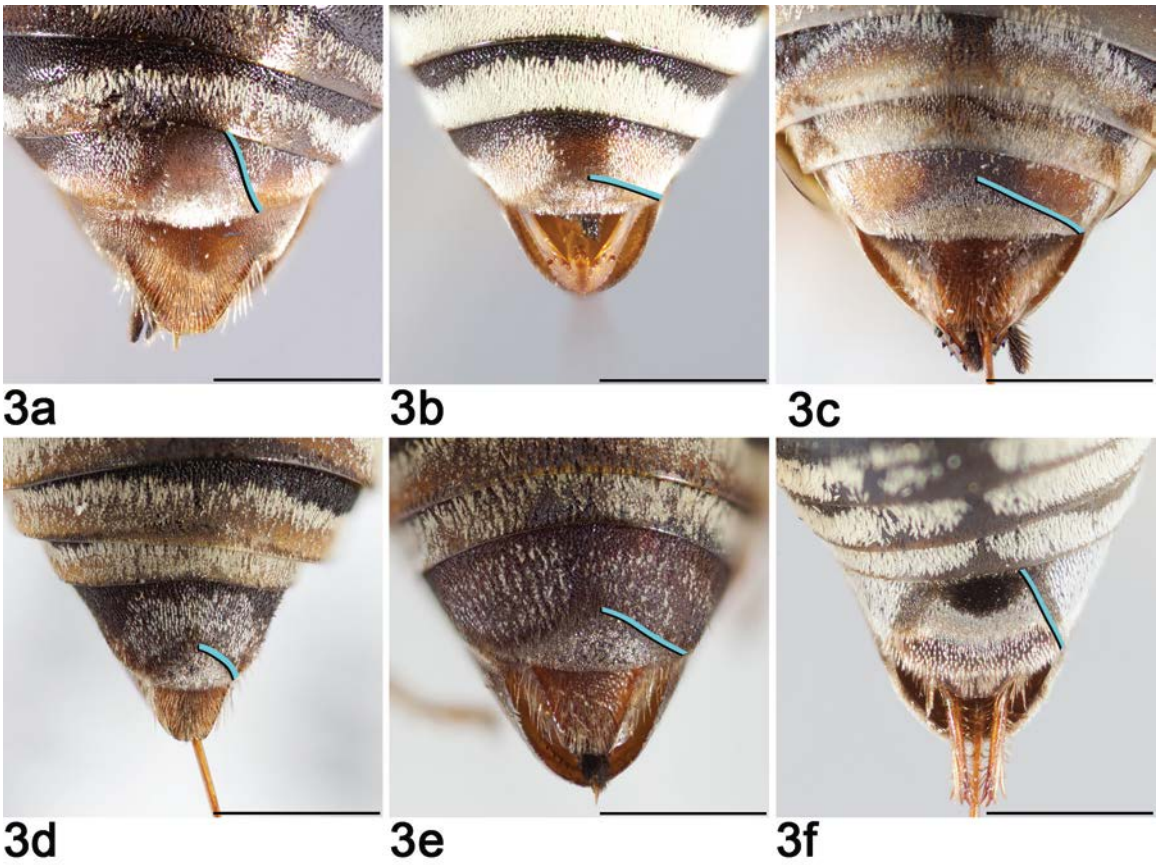



**Figure 3.** Pseudopygidial area of female Epeolini in dorsal view: a) *E. ilicis* (campanulate), b) *E. ainsliei* (lunate and wider than long), c) *E. olympiellus* (lunate and wider than long), d) *E. pusillus* (lunate and nearly as long as wide), e) *E. scutellaris* (lunate and wider than long), and f) *T. epeolurus* (unique and *Epeolus*-like in having a transverse, curved band of silvery setae). Scale bars = 1 mm. The pseudopygidial area is indicated by an area elevated from the rest of the tergum covered partially or entirely in shiny short hairs uniform in length (posteromesad the light blue lines).

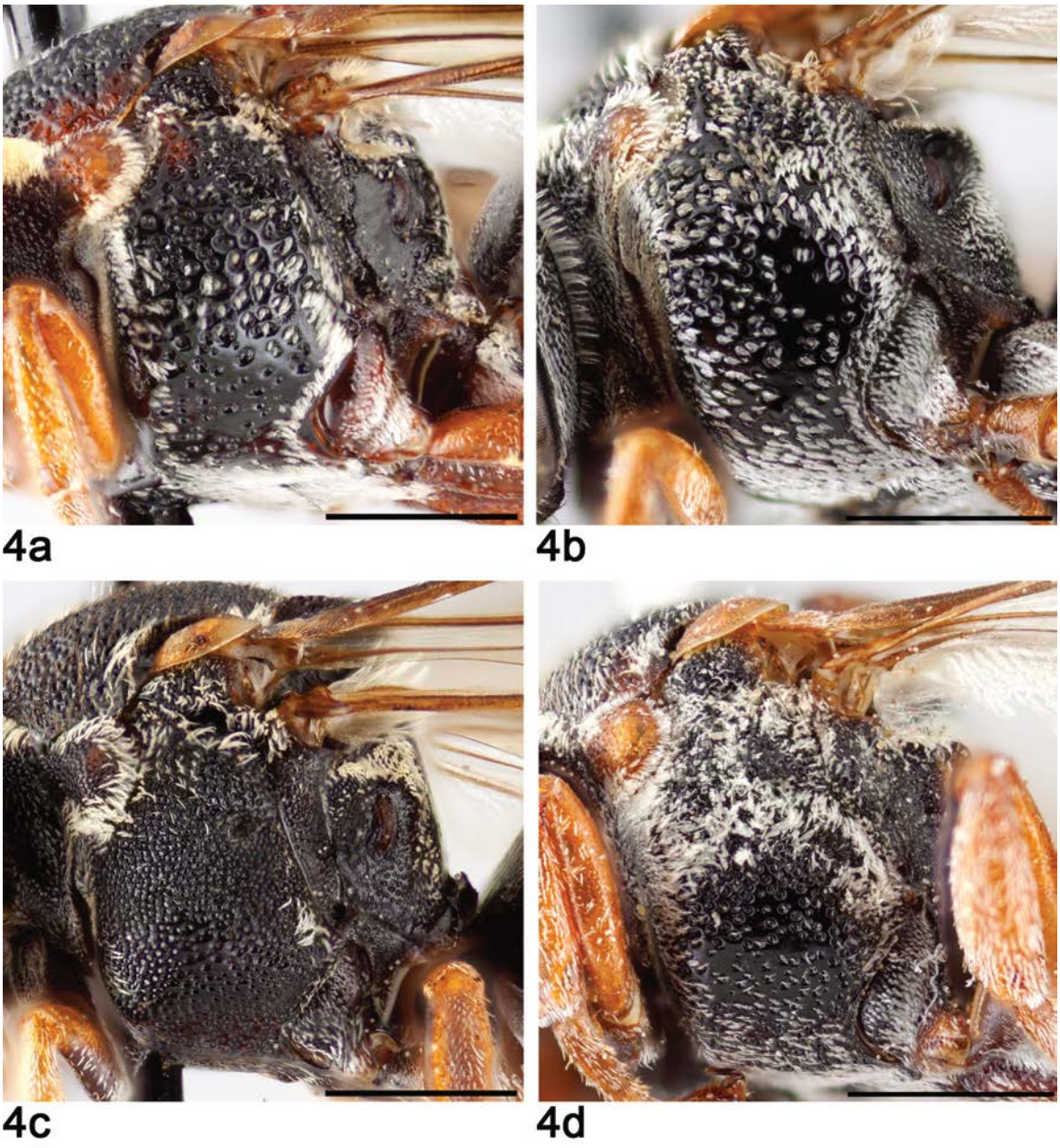



**Figure 4.** Mesopleuron (lateral view) of female a) *E. bifasciatus* showing sparse punctation with punctures larger in upper half than ventrolateral half, b) *E. lectoides* showing sparse punctation with punctures of similar size throughout, c) *E. autumnalis* showing dense punctation with punctures of similar size throughout, and d) *E. interruptus* showing sparse punctation with punctures of similar size throughout. Scale bars = 1 mm.

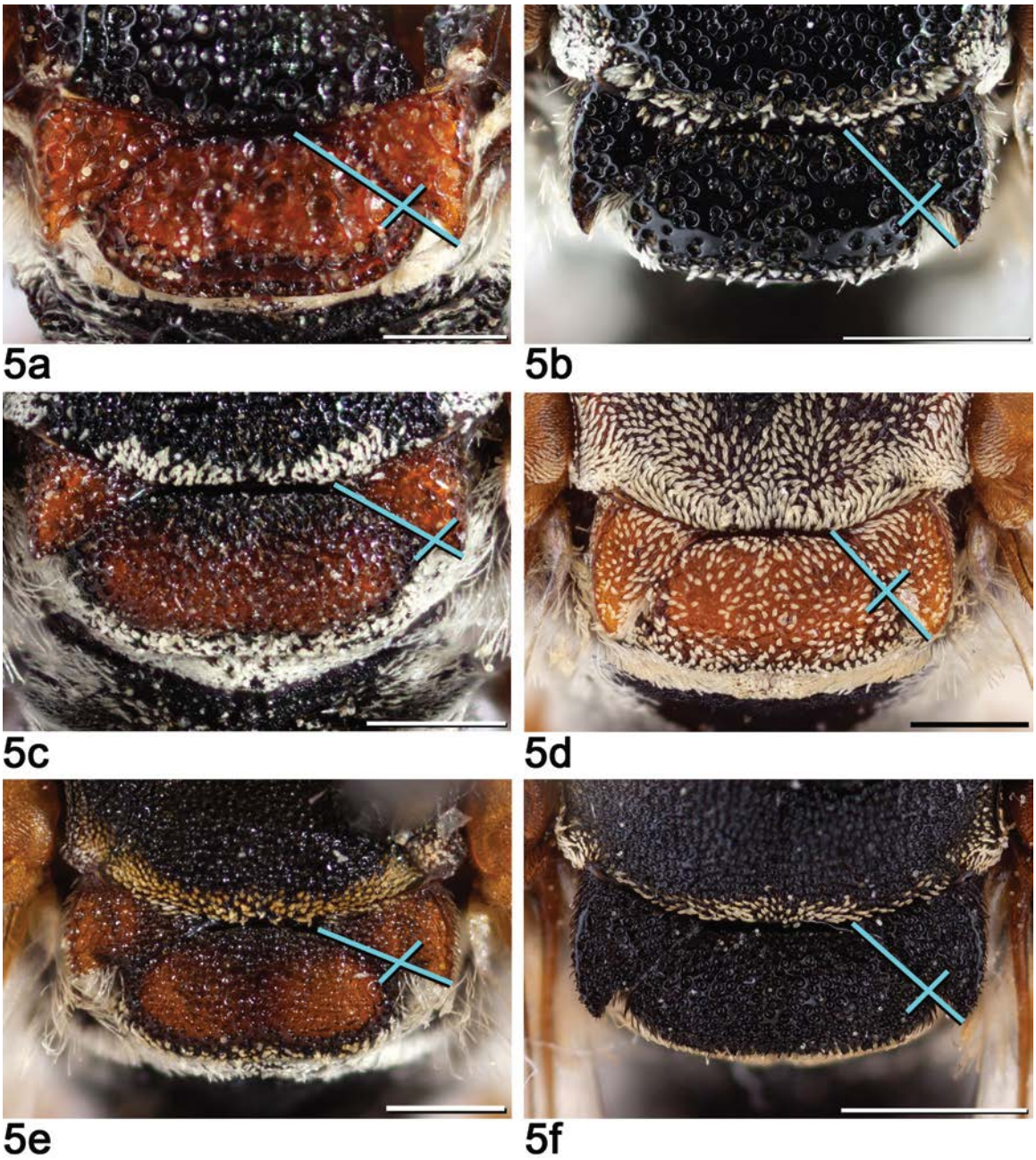



**Figure 5.** Variation in length of free portion of axilla relative to axillar medial length in dorsal view of a) female *E. bifasciatus* (Scale bar = 0.5 mm), b) female *E. lectoides* (Scale bar = 1 mm), c) female *E. interruptus* (Scale bar = 0.5 mm), d) female *E. ainsliei* (Scale bar = 0.5 mm), e) female *E. ilicis* (Scale bar = 0.5 mm), and f) female *E. autumnalis* (Scale bar = 1 mm).


**Figure 6.** Head with frontal area of a) male *E. bifasciatus* showing pair of granulose protrusions and b) female *E. lectoides* without protrusions. Scale bars = 1 mm.


**Figure 7.** Metasoma of a) female *E. bifasciatus* (Scale bar = 1 mm) and b) female *E. lectoides* (Scale bar = 3 mm) in dorsal view.


**Figure 8.** Mesosoma (posterior half in dorsal view) illustrating metanotum that is a) with a blunt median process in female *E. interruptus*, and b) without a process and flat in female *E. minimus*. Scale bars = 0.5 mm.

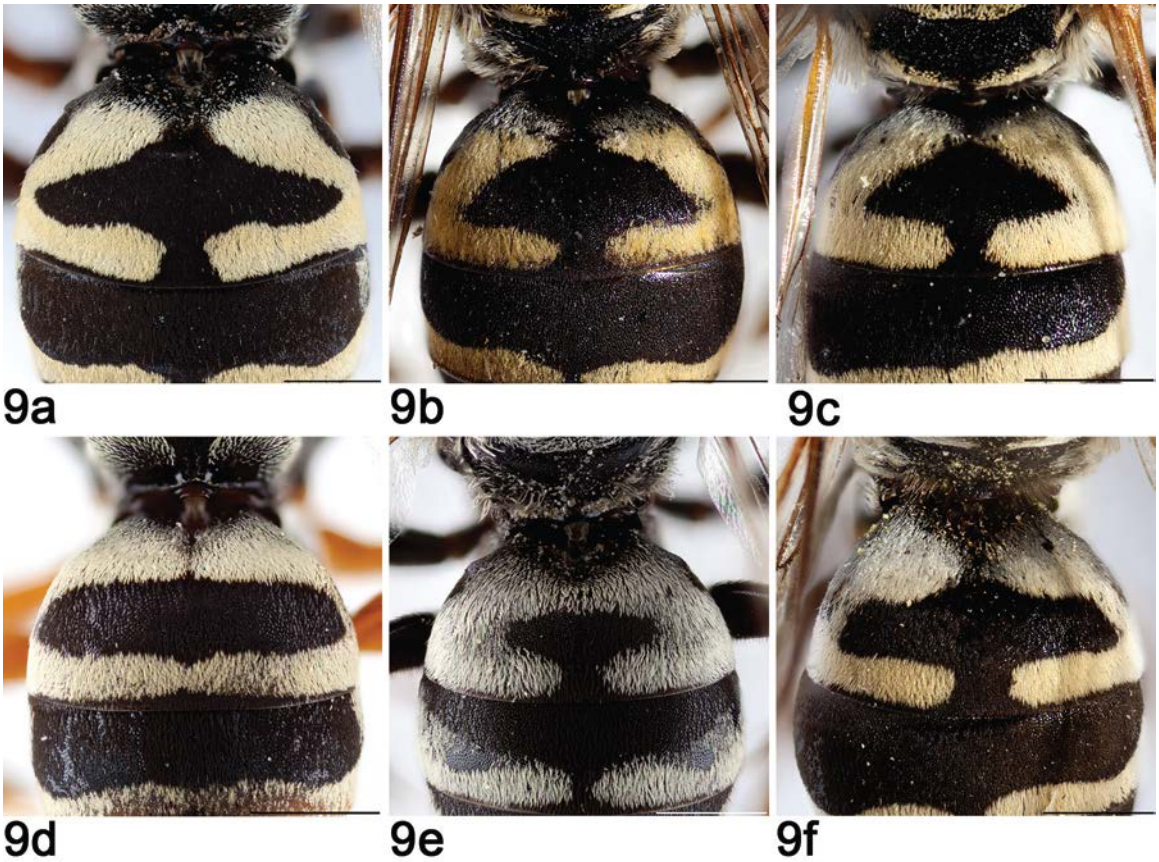



**Figure 9.** T1 at base of metasoma (dorsal view) of a) male *E. interruptus* illustrating triangular discal patch with concave lateral sides, b) female *E. canadensis* illustrating semicircular discal patch, c) male *E. canadensis* illustrating triangular discal patch, d) female *E. pusillus* illustrating wide rectangular discal patch (longitudinal band barely visible in dorsal view), e) female *E. americanus* illustrating narrow quadrangular discal patch, and f) female *E. compactus* illustrating quadrangular discal patch of intermediate width (longitudinal band clearly visible in dorsal view). Scale bars = 1 mm.


**Figure 10.** Lower faces of *Epeolus* spp. showing the mandible a) without a preapical angulation or tooth in female *E. ainsliei*, b) with a preapical tooth in male *E. compactus*, and c) with an obtuse angle appearing like a tooth in female *E. autumnalis*. Scale bars = 0.5 mm.

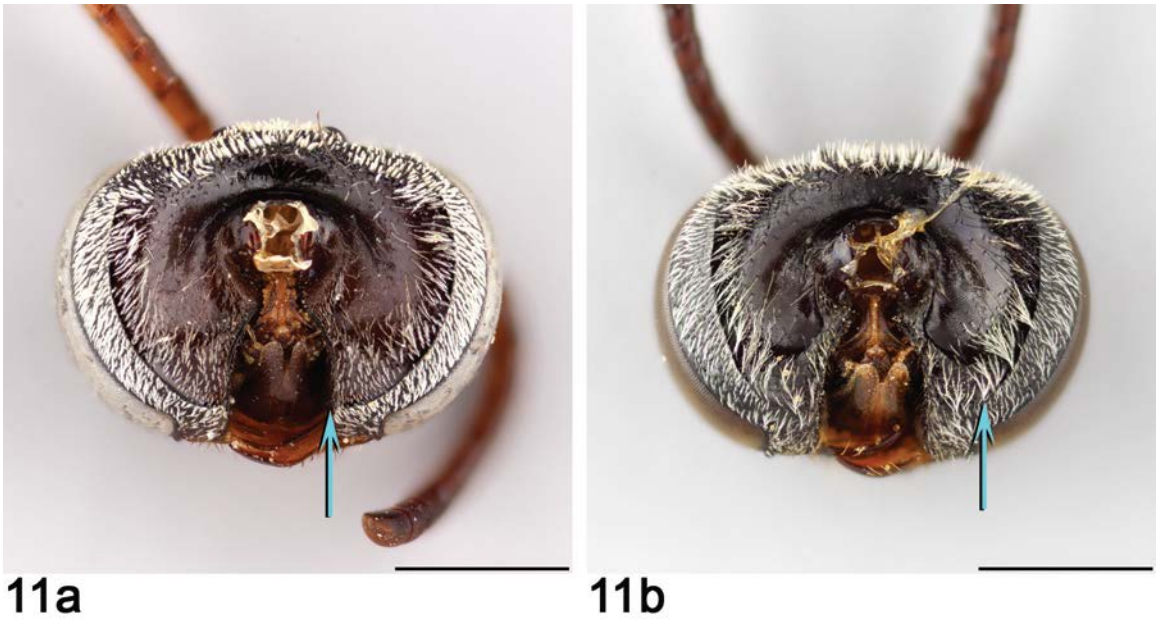



**Figure 11.** Head (posterior view) removed from a) female *E. ainsliei*, in which the preoccipital ridge joins the hypostomal carina, and b) male *E. ilicis*, in which the preoccipital ridge does not join the hypostomal carina (arrow indicates the maximum extent of the carina). Scale bars = 1 mm. Note that these features can be seen without having to detach the head.

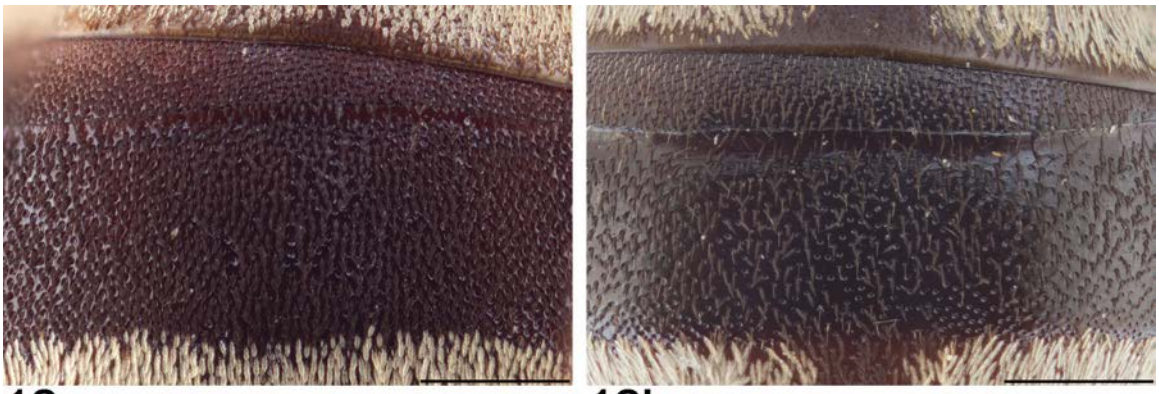



**Figure 12.** T2 (medial portion in dorsal view) of a) female *E. ainsliei* showing dense punctation (i<1d) and b) male *E. ilicis* showing sparser punctation (i=1–2d). Scale bars = 0.5 mm.

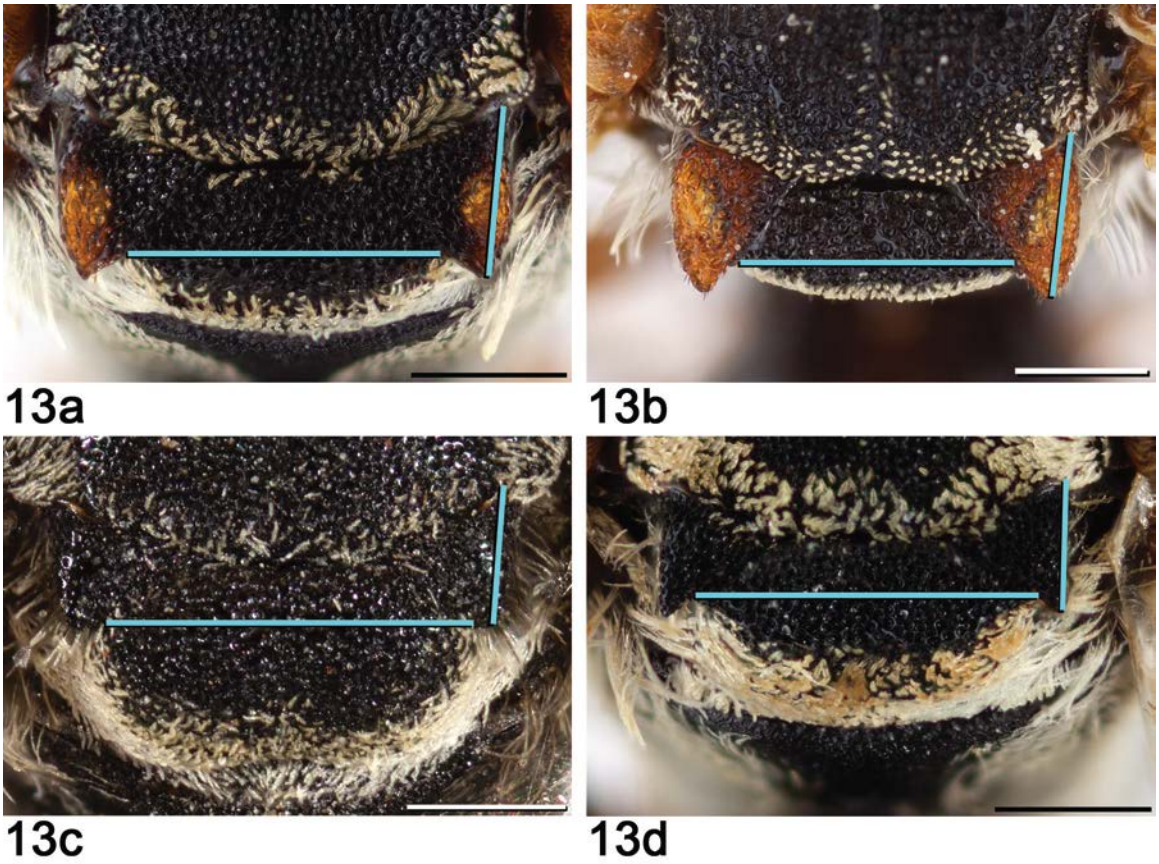



**Figure 13.** Variation in length of lateral margin of axilla versus width of mesoscutellum between axillae posteriorly in dorsal view of a) female *E. pusillus*, b) male *E. scutellaris*, c) female *E. americanus*, and d) female *E. minimus*. Scale bars = 0.5 mm.


**Figure 14.** Antennae (basal portion) of female *Epeolus* spp. illustrating relative length to width of F2: a) *E. americanus*, with F2 as wide as long, or nearly so, and b) *E. olympiellus*, with F2 noticeably longer than wide. Scale bars = 0.5 mm.


**Figure 15.** Variation in mesoscutal pubescence (dorsal view) among males of a) *E. compactus*, b) *E. minimus*, and c) *E. olympiellus*. Scale bars = 1 mm.

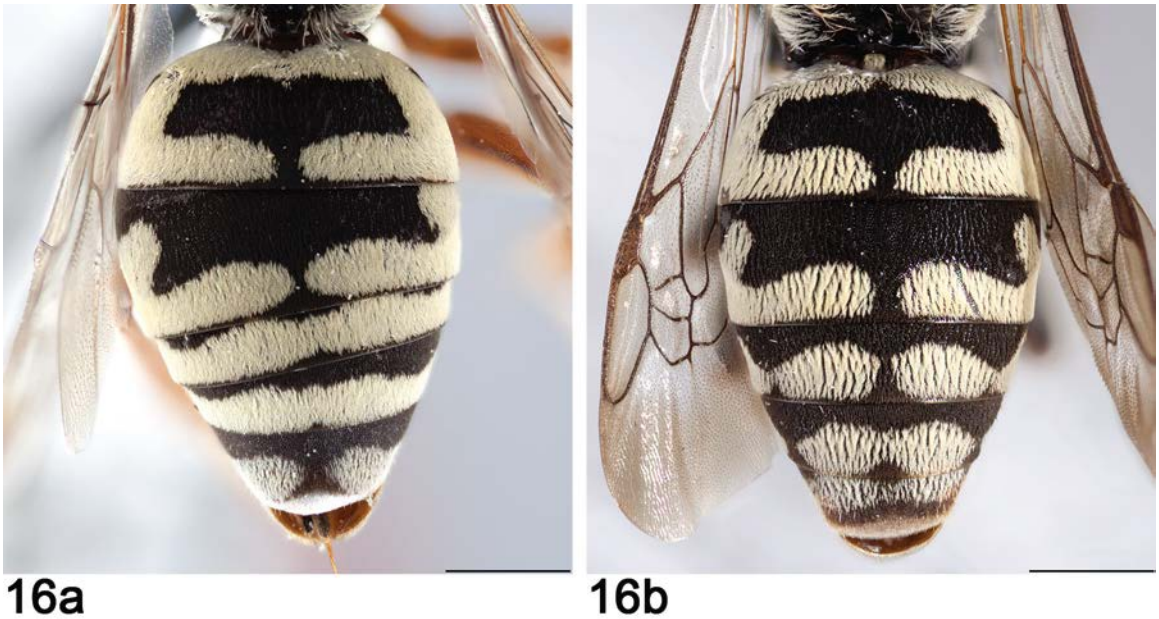



**Figure 16.** Metasoma of female (dorsal view) illustrating variation in fasciae on T3 and T4: a) *E. minimus*, in which T3 and T4 are with complete fasciae, and b) *E. olympiellus*, in which T3 and T4 are with fasciae that are separated or greatly narrowed medially and laterally. Scale bars = 1 mm.


**Figure 17.** Metanotum of male (posterior view) showing a) the presence of a median patch of black tomentum nearly as wide as lateral patches of pale tomentum in *E. canadensis*, and b) the presence of a median interruption of darker tomentum narrower than the width of lighter lateral patches in *E. compactus*. Scale bars = 1 mm.


**Figure 18.** Head of female (frontal view) a) *E. minimus* showing extensive orange colouration on the labrum and antennae, and b) *E. olympiellus*, in which the labrum and antennae are black (except for some small brown markings). Scale bars = 1 mm.

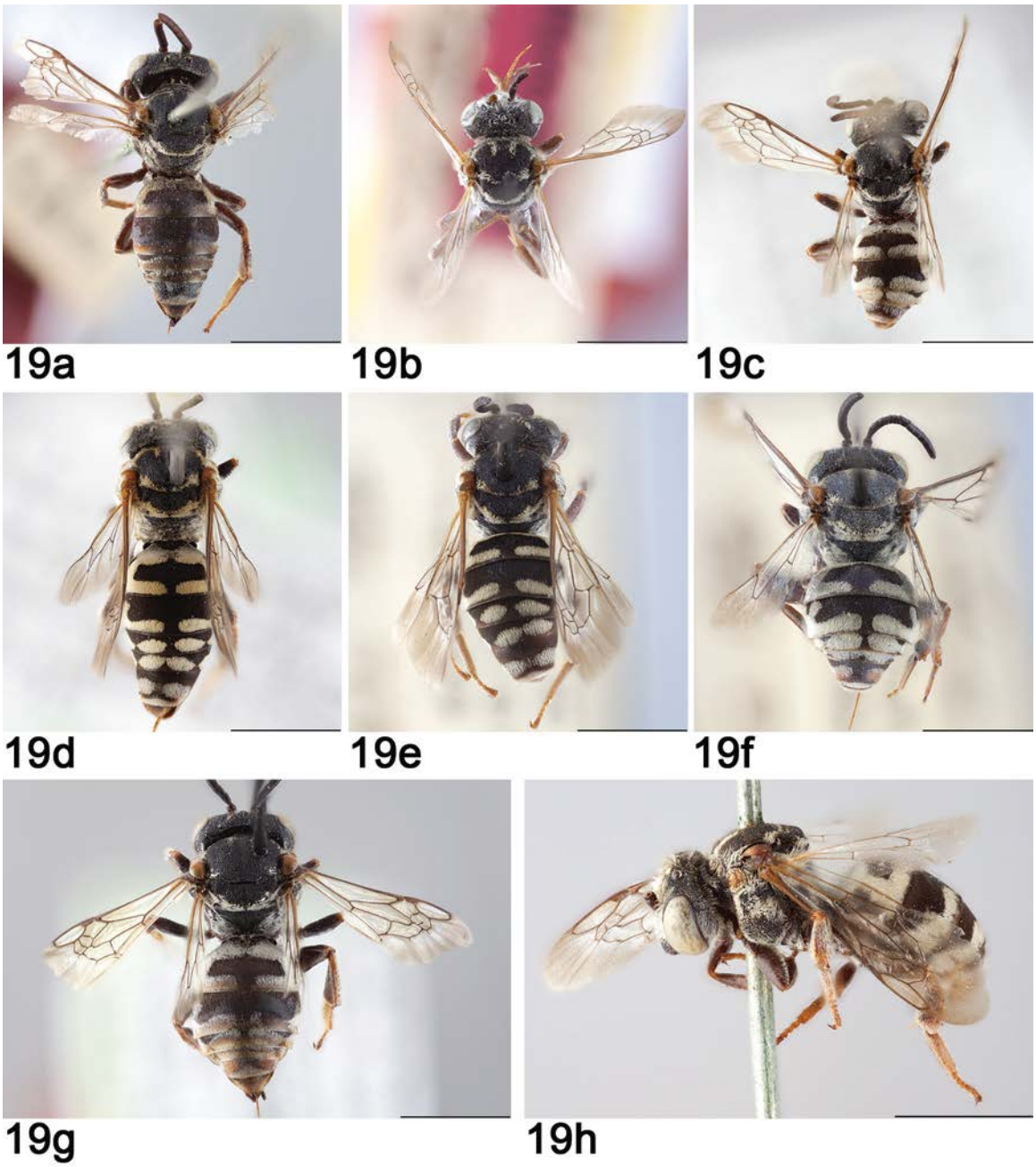



**Figure 19.** A comparison of the holotypes of a) *E. tristicolor*, b) *E. humillimus*, e) *E. rubrostictus*, f) *E. rufomaculatus*, and h) *E. olympiellus* (the species under which the preceding four are being synonymized) to three barcoded specimens (c, d, and g) of *E. olympiellus* illustrating the variability in the "characteristic" features displayed by the type specimens. Scale bars = 3 mm.


**Figure 20.** T5 of female (dorsal view) a) *E. rufomaculatus* holotype (synonymized herein under *E. olympiellus*) and b) barcoded *E. olympiellus* showing ferruginous integument underlying patches of pale tomentum, and c) barcoded *E. olympiellus* showing black integument underlying patches of pale tomentum. Scale bars = 1 mm.

**Plate 1. Female (top) and male (bottom) lateral images. Scale bars = 3 mm.**

A. *Epeolus ainsliei* Crawford, 1932

B. *Epeolus americanus* (Cresson, 1878)

C. *Epeolus autumnalis* Robertson, 1902

D. *Epeolus bifasciatus* Cresson, 1864

**Plate 1. Female (top) and male (bottom) lateral images cont'd. Scale bars = 3 mm.**

E. *Epeolus canadensis* Mitchell, 1962

F. *Epeolus compactus* Cresson, 1878

G. *Epeolus ilicis* Mitchell, 1962

H. *Epeolus interruptus* Robertson, 1900

**Plate 1. Female (top) and male (bottom) lateral images cont'd. Scale bars = 3 mm.**

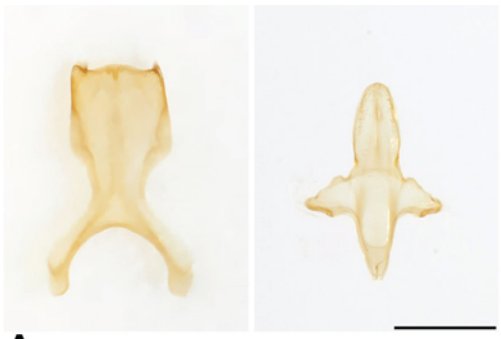
I. *Epeolus lectoides* Robertson, 1901

J. *Epeolus minimus* (Robertson, 1902)

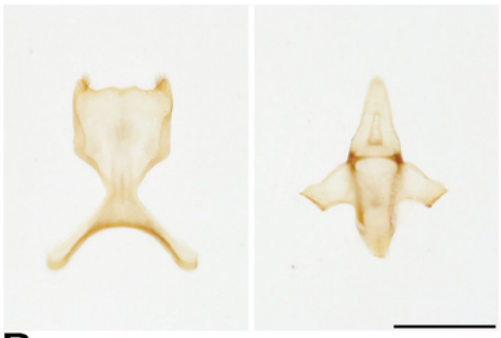
K. *Epeolus olympiellus* Cockerell, 1904

L. *Epeolus pusillus* Cresson, 1864

**Plate 1. Female (top) and male (bottom) lateral images cont'd. Scale bars = 3 mm.**
M. *Epeolus scutellaris* Say, 1824

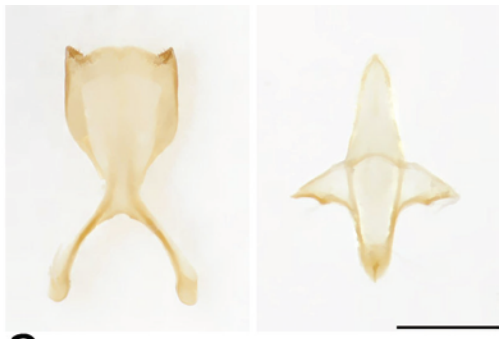


A



B

**Plate 2 - Male S7 (left) and S8 (right), Scale bars = 0.5 mm.**
A. *Epeolus ainsliei* Crawford, 1932
B. *Epeolus americanus* (Cresson, 1878)



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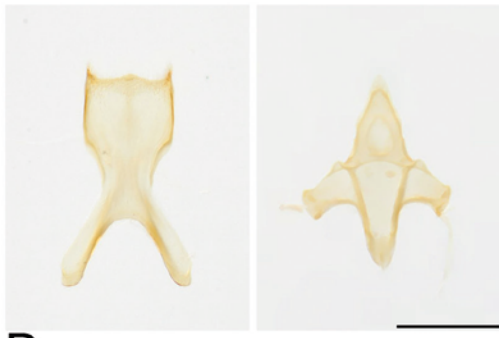
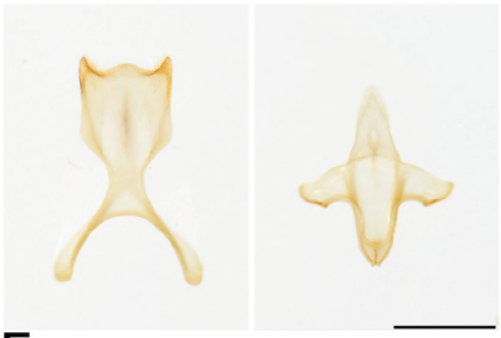


D

C. *Epeolus autumnalis* Robertson, 1902
D. *Epeolus bifasciatus* Cresson, 1864



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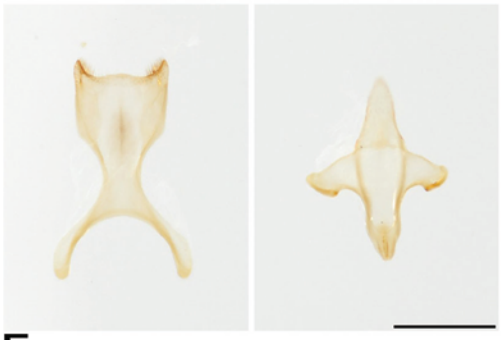
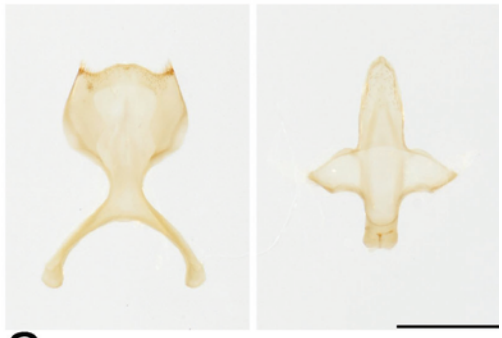
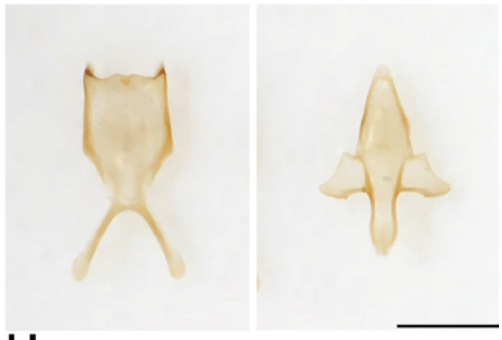


F

E. *Epeolus canadensis* Mitchell, 1962
F. *Epeolus compactus* Cresson, 1878

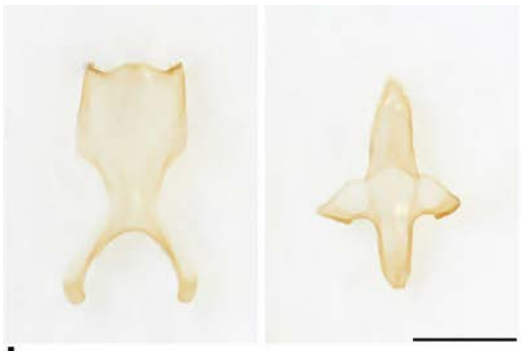


G

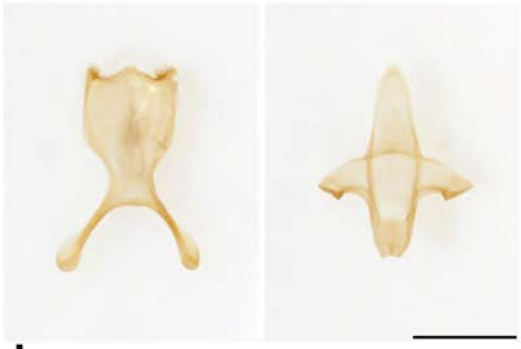


H

G. *Epeolus ilicis* Mitchell, 1962
H. *Epeolus interruptus* Robertson, 1900



I

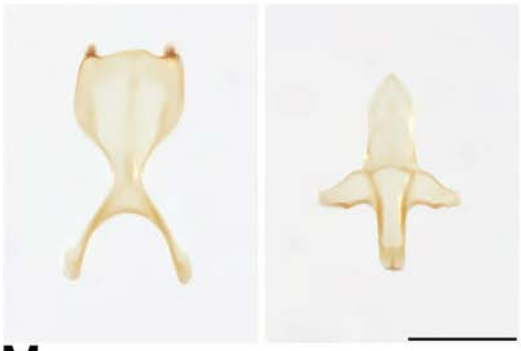


J

**Plate 2 - Male S7 (left) and S8 (right) cont'd, Scale bars = 0.5 mm.**

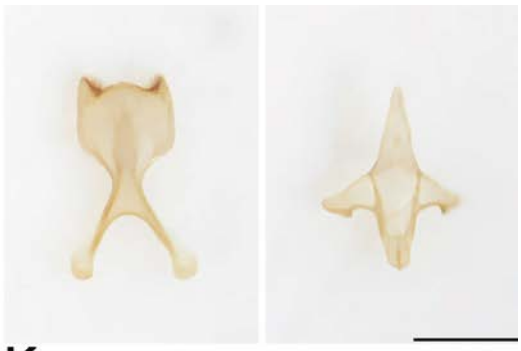
I. *Epeolus lectoides* Robertson, 1901

J. *Epeolus minimus* (Robertson, 1902)

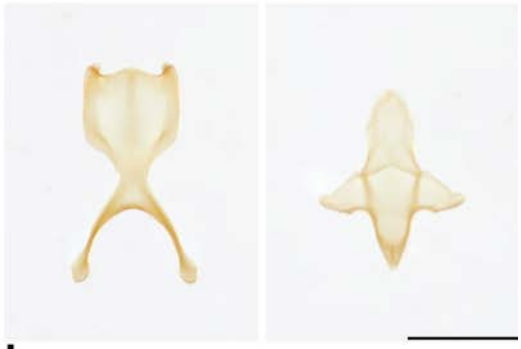


M

M. *Epeolus scutellaris* Say, 1824



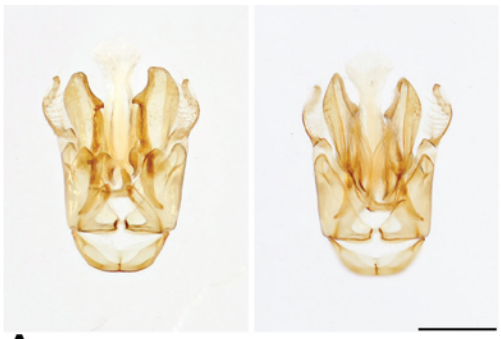
K



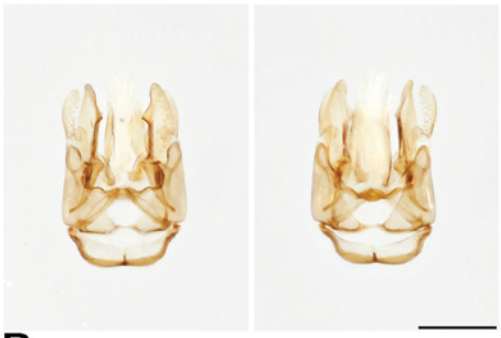
L

K. *Epeolus olympiellus* Cockerell, 1904

L. *Epeolus pusillus* Cresson, 1864

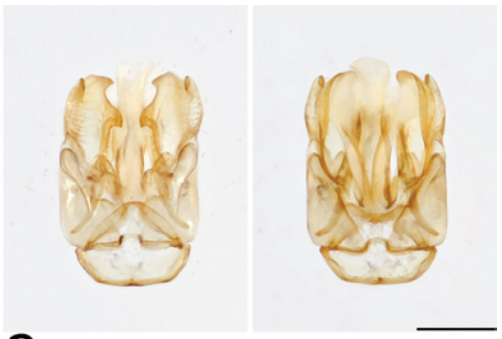


A

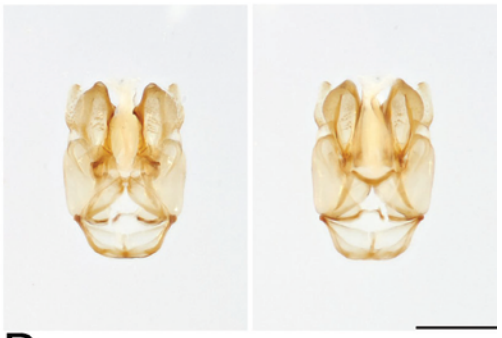


B

**Plate 3 - Male genitalia, ventral view (left), dorsal view (right), Scale bars = 0.5 mm.**
A. *Epeolus ainsliei* Crawford, 1932
B. *Epeolus americanus* (Cresson, 1878)

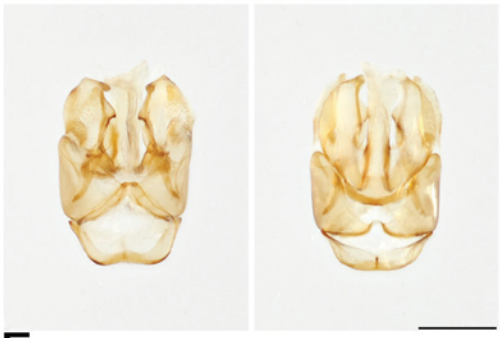


C

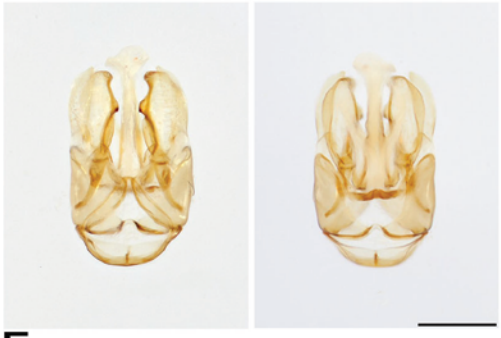


D

C. *Epeolus autumnalis* Robertson, 1902
D. *Epeolus bifasciatus* Cresson, 1864

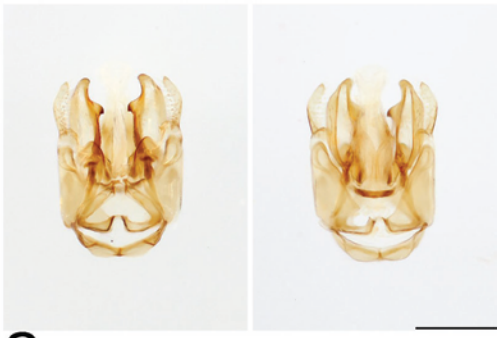


E

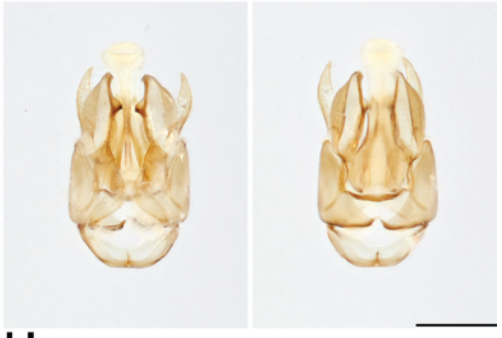


F

E. *Epeolus canadensis* Mitchell, 1962
F. *Epeolus compactus* Cresson, 1878



G



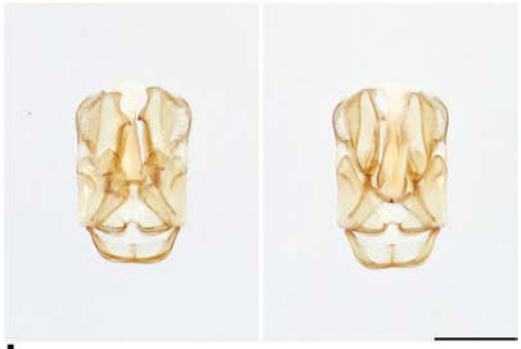
H

G. *Epeolus ilicis* Mitchell, 1962
H. *Epeolus interruptus* Robertson, 1900

I

J

K



L

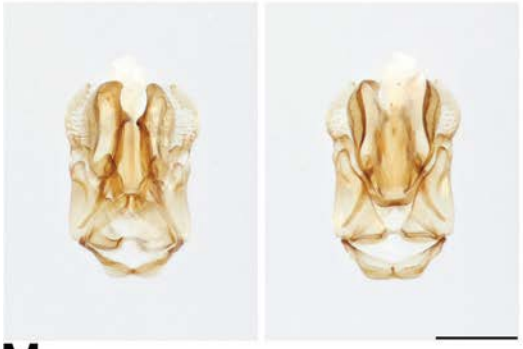
**Plate 3 - Male genitalia, ventral view (left), dorsal view (right) cont'd, Scale bars = 0.5 mm.**

I. *Epeolus lectoides* Robertson, 1901

J. *Epeolus minimus* (Robertson, 1902)

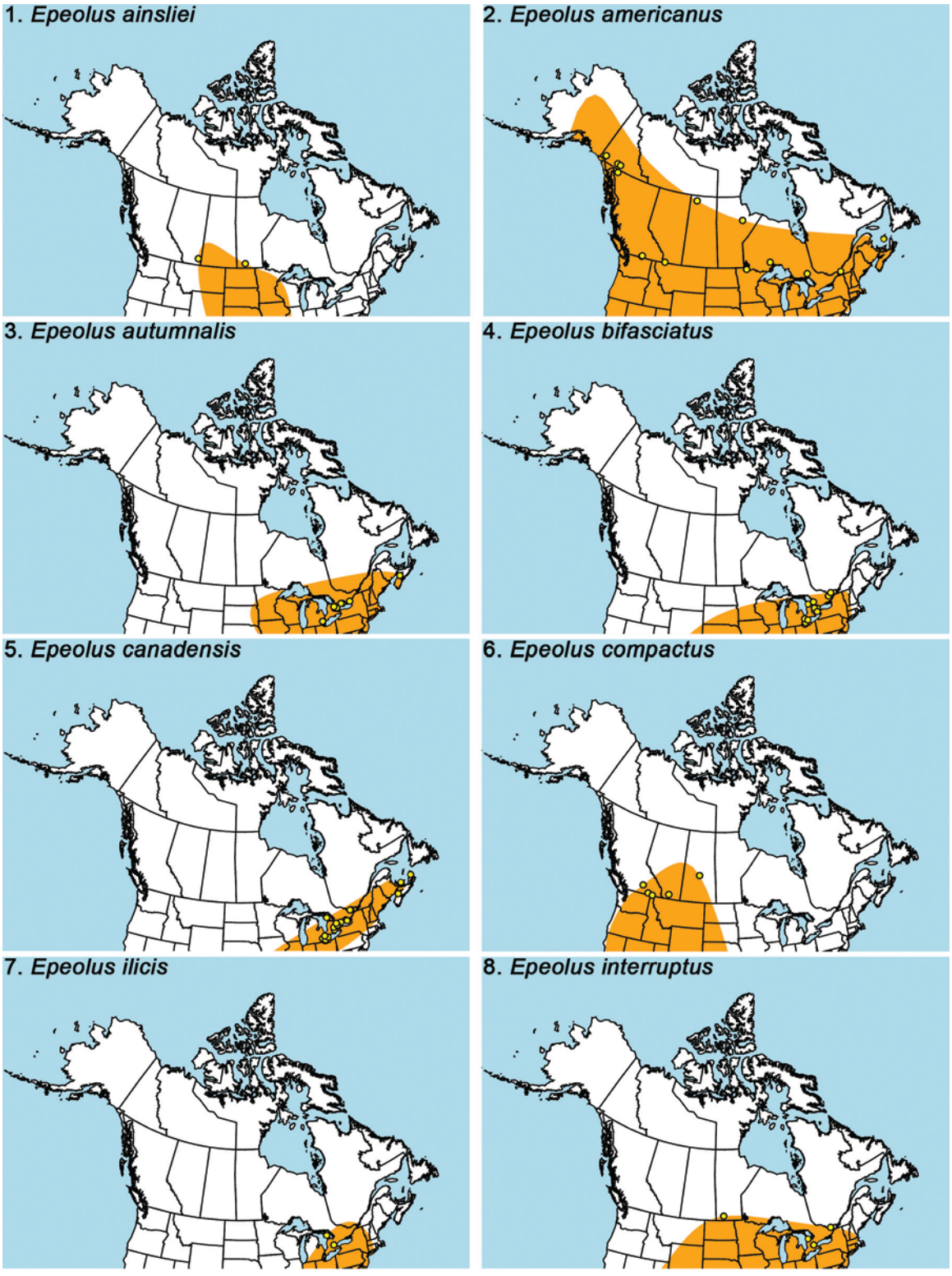
K. *Epeolus olympiellus* Cockerell, 1904

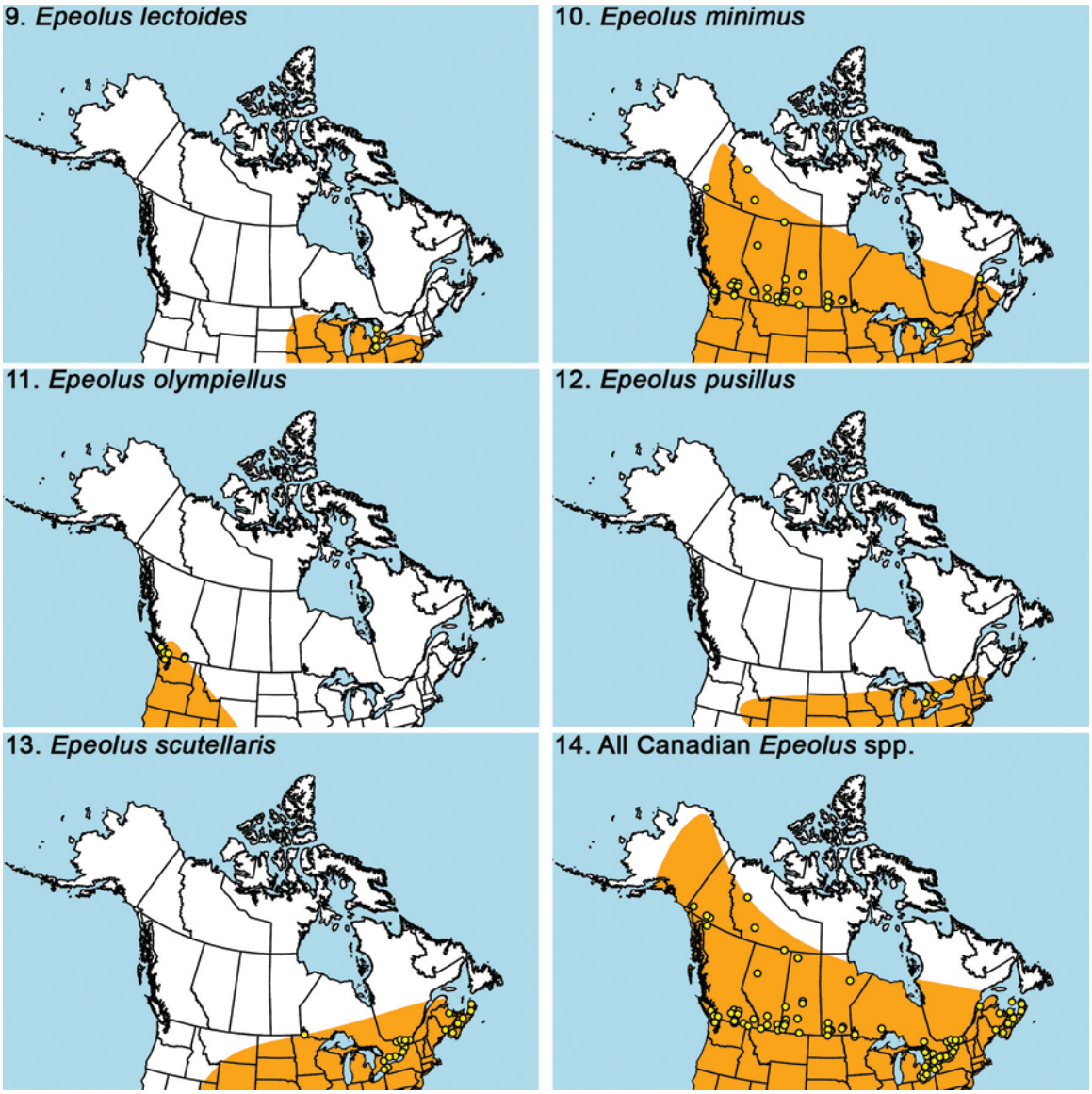
L. *Epeolus pusillus* Cresson, 1864



M

M. *Epeolus scutellaris* Say, 1824


1. Epeolus ainsliei
2. Epeolus americanus
3. Epeolus autumnalis
4. Epeolus bifasciatus
5. Epeolus canadensis
6. Epeolus compactus
7. Epeolus ilicis
8. Epeolus interruptus


9. Epeolus lectoides
10. Epeolus minimus
11. Epeolus olympiellus
12. Epeolus pusillus
13. Epeolus scutellaris
14. All Canadian Epeolus spp.

## Chapter 3: A revision of the cleptoparasitic bee genus *Epeolus* Latreille for Nearctic species, north of Mexico (Hymenoptera, Apidae)

Thomas M. Onuferko[1]

### Abstract

Herein, the cleptoparasitic (cuckoo) bee genus *Epeolus* (Hymenoptera: Apidae) is revised for species occurring in North America, north of Mexico, and an updated checklist of all species known to occur in Canada and the United States of America is provided with comprehensive descriptions, diagnoses, and a single dichotomous key (using the same couplets for both sexes) to aid in their identification. To increase their recognition among North American naturalists, English common names are also proposed for all North American *Epeolus*. A total of 43 species is confirmed as present in the region, 15 of which are newly recognized. The following new species are proposed based on unique morphological (and in most cases also molecular) attributes: *E. andriyi* **sp. n.**, *E. attenboroughi* **sp. n.**, *E. axillaris* **sp. n.**, *E. basili* **sp. n.**, *E. brumleyi* **sp. n.**, *E. chamaesarachae* **sp. n.**, *E. deyrupi* **sp. n.**, *E. diadematus* **sp. n.**, *E. ferrarii* **sp. n.**, *E. gibbsi* **sp. n.**, *E. inornatus* **sp. n.**, *E. nebulosus* **sp. n.**, *E. packeri* **sp. n.**, *E. splendidus* **sp. n.**, and *E. tessieris* **sp. n.** Of the 15, six (*E. axillaris*, *E. brumleyi*, *E. chamaesarachae*, *E. diadematus*, *E. splendidus*, and *E. tessieris*) were identified as new species under different names (*nomina nuda*) in an M.Sc. thesis by Richard L. Brumley in 1965, but until now they have not been formally described. Detailed morphological comparisons with some evidence from DNA barcoding support the following synonymies, one of which **C** was first proposed by Brumley (1965): a) *E. melectimimus* Cockerell and Sandhouse, **syn**. **n**., under *E. asperatus* Cockerell; b) *E. crucis* Cockerell, **syn**. **n**., under *E. compactus* Cresson; c) *E. mesillae palmarum* Linsley, **syn**. **n**., under *E. mesillae* (Cockerell); and d) *E. weemsi* Mitchell, **syn**. **n**., and e) *E. vernalis* Mitchell,

[1] This manuscript has been published and is reprinted here with the publisher's permission: Onuferko, T.M. 2018. A revision of the cleptoparasitic bee genus *Epeolus* Latreille for Nearctic species, north of Mexico (Hymenoptera, Apidae). *ZooKeys* No. 755: 1–185. doi: 10.3897/zookeys.755.23939

**syn**. **n**., under *E. ilicis* Mitchell. Only one member of the almost entirely Neotropical "Trophocleptria group" (*Epeolus bifasciatus* Cresson) is confirmed as occurring north of Mexico, and is widespread East of the Rocky Mountains. Known floral associations are indicated for each species, as are suspected or known host species of *Colletes* Latreille. Evidence is presented that suggests further investigation into the possible synonymy of *Colletes wickhami* Timberlake under *C. scopiventer* Swenk is warranted.

**Key words:** cleptoparasitic bee, DNA barcoding, *Epeolus*, morphology, taxonomic revision

## Introduction

*Epeolus* Latreille (Hymenoptera: Apidae, subfamily Nomadinae) is one of the most widespread genera of cleptoparasitic bees (commonly referred to as cuckoo bees), occurring on all continents except Antarctica and Australia. The genus is also absent from Madagascar, Oceania, and parts of Southeast Asia, regions in which their host genus *Colletes* Latreille (Hymenoptera: Colletidae: Colletinae) is not present (Michener 2007). Other genera in the tribe Epeolini are largely restricted to the Americas, mostly to the Neotropical region. The similarly diverse bee genus *Triepeolus* Robertson has only two representatives in the Palearctic region, whereas *Epeolus* is represented across Africa, Asia, and Europe by about 48 species (Ascher and Pickering 2017). However, the genus is most diverse in North America, with 32 valid species confirmed as occurring north of Mexico before the date of this publication.

For North American species, the taxonomy of *Epeolus* has been in need of revision for some time. While Mitchell's (1962) treatment of the Eastern United States fauna was fairly comprehensive, the Western species have been in much need of attention. In his M.Sc. thesis, Richard L. Brumley (1965) recognized several new species from the Western United States, but his names were never published and are therefore not considered valid. Recently, Onuferko (2017) identified 14 redundant names (most are of Western "species"), which were synonymized under the names of four valid species, but this treatment was limited to the Canadian fauna. The purpose of the present study is to resolve the taxonomy of *Epeolus* occurring in Canada and the USA by naming and describing new species and identifying which accepted names are valid and which are not, thereby standardizing name use, as well as to provide a user-friendly dichotomous

identification key. To help amateur and professional entomologists become more familiar with these bees, English common names are proposed for all North American species of *Epeolus*. An additional objective is to present ecological information in terms of floral and *Colletes* hosts and phenology wherever possible, as well as comprehensive occurrence records to aid those interested in locating and identifying representatives of the species treated herein for further research.

## Materials and methods

To revise *Epeolus* an integrative biosystematics approach was followed, using morphological and molecular evidence to distinguish intraspecific from interspecific variation (as in Gibbs 2009, 2010, 2011, Pauly et al. 2014, Rocha-Filho and Packer 2015, Ferrari 2017, Onuferko 2017). Morphological evidence was prioritized over molecular evidence when the two were not in agreement, as in Gibbs (2009). Sequence data from a 658 bp segment of the mitochondrial cytochrome c oxidase subunit I (COI) gene (DNA barcode, Hebert et al. 2003a, b) were obtained from specimens of nearly all (42 out of 43) species, and 37 have sequences that are barcode compliant (i.e., have met the criteria to be assigned automated barcode index numbers (BINs) given to unique barcode clusters, Ratnasingham and Hebert 2007, 2013). One or two legs were removed from each specimen to be "barcoded", and sent to the Canadian Centre for DNA Barcoding in Guelph, Ontario, Canada for DNA extraction and gene amplification and sequencing. A neighbor-joining (NJ) tree, based on Kimura's two-parameter distance model (Kimura 1980), was used to compare short, non-compliant and barcode-compliant sequences for the purpose of validating species designations of sequenced specimens and checking for contamination errors. Partial and BIN-compliant sequences are published in the "*Epeolus* of North America project" on the Barcode of Life Data Systems website (http://www.barcodinglife.org/) and have been deposited in the GenBank database (see Suppl. material 1 for accession numbers).

Terminology used herein is consistent with that used in the recent treatment of Canadian *Epeolus* (Onuferko 2017), which generally followed Michener (2007), except the terms frontal area and vertexal area are used instead of frons and vertex, respectively. Acronyms used herein (in bold) are as follows. Puncture density is described in terms of interspaces (**i**) relative to the

diameters (**d**) of punctures. Median ocellar diameter (**MOD**) is a comparative unit of measurement for smaller structures. **F** followed by a number represents one of 10 (for female) or 11 (for male) flagellomeres of the antenna. **T** followed by a number represents one of six (for female) or seven (for male) exposed metasomal terga. **S** followed by a number represents one of six (for female) or eight (for male) metasomal sterna. Several terms used in Onuferko (2017), some of which were taken from Rightmyer (2008), are defined here again for clarity, and are indicated in bold. **Length** refers to measurements made along the longitudinal axis of the bee, except in reference to the longitudinal extent of the transverse metasomal fasciae, for which the term **breadth** is used, and **width** refers to measurements made along the lateral axis. The length and width of an anatomical feature refer to its longest and widest margins, respectively, and were recorded at the highest magnification that allowed measurement in ocular micrometer units. The scape was measured without the radicle. In *Epeolus*, the frontal line extends into the supraclypeal area as a pronounced carina on a convex surface, referred to herein as the **frontal keel**. **Paramedian bands** are the paired lines of off-white or yellow tomentum located anteriorly on the mesoscutum of most *Epeolus* species (Fig. 1). The term **bigibbous** is an adjective used in reference to the biconvexities present on the mesoscutellum of *Epeolus* species. The basal and apical fasciae of T1 are often connected by a **longitudinal band** of pale tomentum of varying width. **Discal patch** refers to the discal region of T1 that is typically covered in dark tomentum and is bordered by bands of pale tomentum. This area is not always clearly delineated because the surrounding bands of pale tomentum may be reduced or missing entirely.

The species of *Epeolus* are, with the usual exceptions (differences in the number of antennal flagellomeres, number of exposed metasomal terga, length of the S4 and S5 subapical hairs [usually longer in males], and terminalia) and a few atypical ones, sexually monomorphic. For this reason, separate keys for females and males are not presented, and the few sex-specific features used to distinguish species are indicated as such in the couplets. The key to Nearctic *Epeolus* is heavily based on the structure of the axilla and the bands of pale tomentum forming the basal and apical fasciae on the metasomal terga. To limit the number of steps required to identify all species, efforts were made to make the key as close to fan shaped (evenly bifurcated) as possible, following the recommendations of Walter and Winterton (2007; see also Packer et al. 2016). When possible, couplets were based on more than a single feature (ideally one per tagma) should one be obscured or lost in the specimen being identified. However, avoiding

monothetic couplets was not always possible. In such cases couplets were usually based on mesosomal features that should be visible even in damaged pinned specimens. In couplets that list multiple features, the most important (i.e., reliable) one for achieving a diagnosis is given first whereas features that do not always result in a positive identification (e.g., integument black vs integument black or ferruginous will resolve species with ferruginous but not black integument) are included but given at the end and always preceded by at least one feature that is fully contrasted between both halves of the couplet. The features referenced in the key were imaged. Quite often a single image or image plate was used to illustrate more than one feature, so a number of figures were cited two or more times within the key and elsewhere in the present monograph. As a result, it was not possible to put most illustrations near the couplets without duplicating them, and for practical reasons multiple versions of the same figures are not included herein. Many couplets rely on precise comparative measurements, and the key is meant to be used with the aid of an eyepiece graticule. None of the couplets require specimens to be dissected. Although the male S7, S8, and genital capsules of nearly all species were examined (except those represented by very few male specimens), the variation among them is minimal (illustrated in part in plates 2 and 3 in Onuferko 2017), and the terminalia have not proven useful in separating similar-looking species. Consequently, they have not been illustrated or imaged. The illustrations presented to aid in the identification of *Epeolus* species are my own. Images were taken with a digital camera (Canon EOS 40D SLR) using the Visionary Digital macro-imaging BK PLUS Lab System, focus stacked in Helicon Focus, and edited in Adobe Photoshop and PaintShop Pro.

Species descriptions follow the format of Onuferko (2017). A full description of the primary type specimen of each species is provided, except for the species occurring in Canada that were recently redescribed in Onuferko (2017). The physical name-bearing type specimens of all described North American *Epeolus* were seen and thoroughly examined, including those whose names are no longer considered valid, except in the case of *E. mercatus* Fabricius, for which the original type material cannot be traced and description is so insufficiently detailed that it is unclear if the species is an *Epeolus* or *Triepeolus* (Rightmyer 2008). Since most *Epeolus* species to date were described from female specimens, new species described herein are generally represented by a female holotype, male allotype, and paratypes. Given that *Epeolus* is a genus of largely sexually monomorphic species, descriptions of the sex opposite that of the

name-bearing type list only key differences to avoid unnecessary duplication of text. In many, but not all, cases it is the female that is fully described. I have opted to propose new names for the species Brumley (1965) discovered rather than validate the ones he used. This will ensure that it is clear who made designations of type specimens (i.e., specimens used as types by Brumley (1965) and me have both our type labels, those unavailable to me but designated as types by Brumley (1965) have only his labels, and those seen exclusively by me and given type status have only my labels). This will also eliminate any possible confusion that could arise if Brumley's (1965) names are published and registered in ZooBank long after their first appearance in his thesis.

The proposed common name for each species reflects its scientific name, which in most cases was easy to translate into English. Since there are many genera of cuckoo bees, epeolus is used herein as the common name for the genus instead of cuckoo bee or more specific but cumbersome names like Colletes cuckoo bee or polyester bee cuckoo bee.

Among the material examined were representatives of *Epeolus* from all Canadian provinces and territories except Newfoundland and Labrador and Nunavut, and all but six (Connecticut, Delaware, Kentucky, Rhode Island, Tennessee, and West Virginia) of the 49 states in the continental U.S. where the genus is expected to occur. Also examined were *Epeolus* records from 17 states in Mexico, and their data are included for species confirmed as occurring north of the Mexico–United States border. All examined records are presented in Suppl. material 1. Specimens were made available for study by curators and collections managers (in parentheses) from the following institutions:

**ABS—**Archbold Biological Station, Venus, FL (M. Deyrup);

**AMNH—**American Museum of Natural History, New York, NY (J.G. Rozen, Jr. and C. Smith);

**ANSP—**Academy of Natural Sciences of Drexel University, Philadelphia, PA (J. Weintraub);

**AUMNH—**Auburn University Museum of Natural History, Auburn, AL (C.H. Ray);

**BBSL—**Utah State University USDA Bee Biology and Systematics Laboratory, Logan, UT (T.L. Griswold);

**BIML—**Patuxent Wildlife Research Center USGS Native Bee Inventory and Monitoring Lab, Laurel, MD (S. Droege);

**CAS—**California Academy of Sciences, San Francisco, CA (B. Fisher and R. Zuparko);

**CNC—**Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, ON (S. Cardinal); **CTMI—**Central Texas Melittological Institute, Austin, TX (J.L. Neff);
**CUIC—**Cornell University Insect Collection, Ithaca, NY (J. Dombroskie);
**CUM—**University of Colorado Museum of Natural History, Boulder, CO (V. Scott);
**DEBU—**University of Guelph Insect Collection, Guelph, ON (S.A. Marshall);
**EMEC—**University of California Essig Museum of Entomology, Berkeley, CA (P. Oboyski);
**FMNH—**Field Museum of Natural History, Chicago, IL (C. Maier);
**FSCA—**Florida State Collection of Arthropods, Gainesville, FL (K. Schnepp and P.E. Skelley);
**INHS—**Illinois Natural History Survey, Champaign, IL (C. Grinter);
**JBWM—**University of Manitoba J.B. Wallis / R.E. Roughley Museum of Entomology, Winnipeg, MB (J. Gibbs);
**KUNHM—**University of Kansas Biodiversity Institute and Natural History Museum, Lawrence, KS (M.S. Engel and J. Thomas);
**LACM—**Natural History Museum of Los Angeles County, Los Angeles, CA (B.V. Brown and G.A. Kung);
**MCZ—**Harvard University Museum of Comparative Zoology, Cambridge, MA (P.D. Perkins);
**NCSU—**North Carolina State University Insect Museum, Raleigh, NC (R. Blinn);
**NHMUK—**Natural History Museum, London, United Kingdom (D. Notton);
**PCYU—**Packer Collection at York University, Toronto, ON (L. Packer);
**ROM—**Royal Ontario Museum, Toronto, ON (A. Guidotti);
**RSKM—**Royal Saskatchewan Museum, Regina, SK (C. Sheffield);
**UCBME—**University of California Bohart Museum of Entomology, Davis, CA (S. Heydon and T.J. Zavortink);
**UCR—**University of California Entomology Research Museum, Riverside, CA (D. Yanega); and
**USNM—**U.S. National Entomological Collection, National Museum of Natural History, Washington, D.C. (S.G. Brady and B. Harris).

In lists of examined specimens, semi-colons separate records from different localities. Otherwise, commas are used between records from the same locality that are associated with a different collection date, collector(s), and/or repository. In such cases, the locality is not repeated and a comma appears after the specimen repository and before the collection date of the next

record. If only the collection day and month were given, then "????" was used for the missing year. If the collection year was given to two digits but the century or millennium could not be inferred (e.g., from knowing who the collector was and the period in which he/she would have conducted field work), the two-digit year is still indicated but with "??" in front. All GPS coordinates indicated herein are taken directly from specimen labels. For approximate coordinates obtained post hoc for specimens with imprecise locality records used to construct range maps, see Suppl. material 1. For species reported from Canada, only total numbers of females and males from each province or state are shown for examined non-type specimens if the same records have already been published (Onuferko 2017).

Range maps were constructed as in Onuferko (2017) in RStudio (version 1.0.44) using the packages maptools (Bivand and Lewin-Koh 2014), raster (Hijmans 2014), rgdal (Bivand et al. 2014), and rgeos (Bivand and Rundel 2014) installed in R (version 3.3.2) (R Core Team 2016). The shapefiles used to plot projected maps of Canada, Mexico, and the USA were obtained from Statistics Canada (2015), DIVA-GIS (http://www.diva-gis.org/gdata), and the U.S. Census Bureau (2015), respectively.

Floral associations are given for each species based on photo records, observations, and specimen labels. Records published in Onuferko (2017) are not repeated here, but they are included in Suppl. material 1. All floral records were checked against The Plant List (http://www.theplantlist.org/) to ensure that the scientific nomenclature is up to date.

## Taxonomy

### *Epeolus* Latreille, 1802

*Epeolus* Latreille, 1802: 427. Type species: *Apis variegata* Linnaeus, 1758, by monotypy.
*Trophocleptria* Holmberg, 1886: 233, 275. Type species: *Trophocleptria variolosa* Holmberg, 1886, by monotypy.
*Epeolus* (*Diepeolus*) Gribodo, 1894: 80. Type species: *Epeolus giannellii* Gribodo, 1894, by monotypy.
*Epeolus* (*Monoepeolus*) Gribodo, 1894: 80. Type species: *Apis variegata* Linnaeus, by monotypy.

*Pyrrhomelecta* Ashmead, 1899: 66. Type species: *Epeolus glabratus* Cresson, 1878, by original designation and monotypy.
*Argyroselenis* Robertson, 1903: 284. Type species: *Triepeolus minimus* Robertson, 1902, by original designation and monotypy.
*Oxybiastes* Mavromoustakis, 1954: 260. Type species: *Oxybiastes bischoffi* Mavromoustakis, 1954, by original designation and monotypy.

In his original description, Latreille (1802) did not explain the etymology of *Epeolus*, but it seems likely that the name is a diminutive of Epeus/Epeius, the soldier in Greek mythology to whom building the Trojan Horse is attributed, and that it was inspired by the sinister nature of these cleptoparasitic bees. This was the first genus of Epeolini described, and 'epeolus' has since become the root in the names of many other nomadine and non-nomadine genera and tribes (e.g., *Epeoloides* Giraud (Osirini), *Parepeolus* Ducke (Osirini), Protepeolini, *Pseudepeolus* Holmberg (Epeolini), etc.).

Several species of *Epeolus* were previously described as belonging to different genera, in particular *Triepeolus*. On account of Rightmyer's (2008) revision of *Triepeolus*, the generic placement of species that were once erroneously switched has been corrected. A few North American species were (initially or at some point in the past) described as belonging to genera that are no longer considered valid, including *Argyroselenis* Robertson, *Phileremus* (the name is a synonym of *Ammobates* Latreille subgenus *Ammobates* Latreille s. str. in Michener 2007), and *Pyrrhomelecta* Ashmead. These represented unnatural groupings of species by shared homoplasious morphological features: if the fore wing has two submarginal cells (*Phileremus*) instead of the usual three, if the maxillary palpus is three-segmented (*Argyroselenis*) rather than two-segmented (both states occur within *Epeolus* and Thalestriina, Rightmyer 2004), and if there is extensive red versus black integument coloration and reduced pubescence (*Pyrrhomelecta*).

Species of *Epeolus* are small to moderate-sized (body length 5.5–10.0 mm) relatively robust cleptoparasitic (epeoliform) bees. In North America, *Epeolus* may be confused with *Triepeolus*, which it resembles in general appearance, although *Triepeolus* may attain a much larger size (body length up to 18 mm in some species, Rightmyer 2008). The only other North American epeoline genus, *Odyneropsis* Schrottky, is rare (known only from the American Southwest) (Griswold and Parker 1999) and more likely to be confused with vespid wasps

(hence the root ‘odynerus’) rather than *Epeolus*. Comprehensive overviews of the distinguishing features of *Epeolus* in reference to all other Epeolini are provided in Rightmyer (2004) and Michener (2007).

**Diagnosis for *Epeolus* in North America (Canada and the United States).** Diagnostic for female *Epeolus* is a very distinct S6, which is usually retracted except sometimes for a pair of convergent spatulate lateral apical processes bearing setae modified into minute, pointed denticles (Onuferko 2017, Fig. 2A & B). Basally, the processes are separated by a large lobe-like disc, which in *Triepeolus* is reduced to a narrow transverse bar. In both *Triepeolus* (Onuferko 2017, Fig. 2C & D) and *Odyneropsis*, the lateral apical processes are subparallel and bear coarse, spine-like setae. Additionally, females may be separated on the basis of the pseudopygidial area (the apicomedial region of T5 that changes slope from the rest of the tergum), which in *Epeolus* is covered in a silvery band of short apically rounded setae. In *Triepeolus*, the pseudopygidial area is usually longer than in *Epeolus* and in most species the setae reflect a golden color. The T5 in female *Odyneropsis* is unique in that it is broadly notched posteriorly and has a distinct middorsal depressed area in the shape of a pointed oval outlined by ridges (Rightmyer 2004, Fig. 180A).

Male *Epeolus* are more difficult to diagnose. As in females, the body lacks integumental white or yellow areas but the mesosoma and usually other tagmata have short appressed plumose white and/or yellow setae; the maxillary palpus is two or three segmented; the inner margins of the compound eyes are distinctly convergent below; the axilla is produced to a rounded lobe or angle or spine (i.e., not continuing the contour of the mesoscutellum); the distitarsi of all legs have arolia; the fore wing usually has three submarginal cells (if with two, then the second is at least nearly as long as the first), and the marginal cell is apically removed from the wing margin and much longer than the stigma; and a pygidial plate is present. In male *Epeolus*, the pygidial plate in most species is broadly rounded posteriorly (Fig. 2B); in *Odyneropsis* and *Triepeolus* it is usually more elongate and with a median constriction (Fig. 2F). It should be noted that males of some species of *Epeolus* in North America (notably *E. australis* Mitchell, *E. flavofasciatus* Smith, and some males in the “*americanus* group”) have a very narrow and distinctly *Triepeolus*-like pygidial plate (Fig. 2A, C, & D), as opposed to the more broadly rounded/subtruncate pygidial plate typically associated with male *Epeolus* (Fig. 2B). The presence of a preapical tooth

of the mandible (Fig. 3B, C, D, & F) (often hidden from view because the mandibles are usually closed) confirms these and other species as *Epeolus*; all *Triepeolus* and only some *Epeolus* (in North America *E. ainsliei*, *E. erigeronis*, *E. ilicis*, *E. inornatus*, and *E. zonatus*) lack one (Fig. 3A & E) (Rightmyer 2004).

**List of species with their proposed common names**

*Epeolus ainsliei* Crawford, 1932 – Ainslie's epeolus
*Epeolus americanus* (Cresson, 1878) – American epeolus
*Epeolus andriyi* Onuferko, sp. n. – Andrew's epeolus
*Epeolus asperatus* Cockerell, 1909 – rough epeolus
*Epeolus attenboroughi* Onuferko, sp. n. – Attenborough's epeolus
*Epeolus australis* Mitchell, 1962 – southern epeolus
*Epeolus autumnalis* Robertson, 1902 – fall epeolus
*Epeolus axillaris* Onuferko, sp. n. – spiny epeolus
*Epeolus banksi* (Cockerell, 1907) – Banks' epeolus
*Epeolus barberiellus* Cockerell, 1907 – Barber's epeolus
*Epeolus basili* Onuferko, sp. n. – Basil's epeolus
*Epeolus bifasciatus* Cresson, 1864 – two-banded epeolus
*Epeolus brumleyi* Onuferko, sp. n. – Brumley's epeolus
*Epeolus canadensis* Mitchell, 1962 – Canada epeolus
*Epeolus carolinus* Mitchell, 1962 – Carolina epeolus
*Epeolus chamaesarachae* Onuferko, sp. n. – five eyes crowned epeolus
*Epeolus compactus* Cresson, 1878 – compact epeolus
*Epeolus deyrupi* Onuferko, sp. n. – Deyrup's epeolus
*Epeolus diadematus* Onuferko, sp. n. – Texas crowned epeolus
*Epeolus erigeronis* Mitchell, 1962 – fleabane epeolus
*Epeolus ferrarii* Onuferko, sp. n. – Ferrari's epeolus
*Epeolus flavofasciatus* Smith, 1879 – yellow-banded epeolus
*Epeolus floridensis* Mitchell, 1962 – Florida epeolus
*Epeolus gibbsi* Onuferko, sp. n. – Gibbs' epeolus

*Epeolus glabratus* Cresson, 1878 – smooth epeolus
*Epeolus howardi* Mitchell, 1962 – Howard's epeolus
*Epeolus ilicis* Mitchell, 1962 – holly epeolus
*Epeolus inornatus* Onuferko, sp. n. – inornate epeolus
*Epeolus interruptus* Robertson, 1900 – interrupted epeolus
*Epeolus lectoides* Robertson, 1901 – Eastern prized epeolus
*Epeolus lectus* Cresson, 1878 – Great Plains prized epeolus
*Epeolus mesillae* (Cockerell, 1895) – Mesilla epeolus
*Epeolus minimus* (Robertson, 1902) – least epeolus
*Epeolus nebulosus* Onuferko, sp. n. – clouded epeolus
*Epeolus novomexicanus* Cockerell, 1912 – New Mexico epeolus
*Epeolus olympiellus* Cockerell, 1904 – Olympia epeolus
*Epeolus packeri* Onuferko, sp. n. – Packer's epeolus
*Epeolus pusillus* Cresson, 1864 – dwarf epeolus
*Epeolus rufulus* Cockerell, 1941 – reddish epeolus
*Epeolus scutellaris* Say, 1824 – shield-backed epeolus
*Epeolus splendidus* Onuferko, sp. n. – polished epeolus
*Epeolus tessieris* Onuferko, sp. n. – Tessier's epeolus
*Epeolus zonatus* Smith, 1854 – white-banded red epeolus

**1. *Epeolus ainsliei* Crawford, 1932**
Figs 3A, 4, 5, & 95A

*Epeolus ainsliei* Crawford, 1932. Proc. Entomol. Soc. Wash. 34: 74 (♀).

**Diagnosis.** The following morphological features in combination can be used to tell *E. ainsliei* apart from all other North American *Epeolus*: the mandible lacks a preapical angle or tooth and the preoccipital ridge joins the hypostomal carina. In some specimens of *E. scutellaris*, the preoccipital ridge joins or nearly joins the hypostomal carina, in which case it is separated from the hypostomal carina by less than 1 MOD at its terminal, but the species has a blunt, obtuse preapical tooth on the mandible and the axillae are relatively straight along the medial margin

whereas in *E. ainsliei* the free portion is distinctly hooked. *Epeolus ainsliei* is also very similar to *E. attenboroughi* and *E. rufulus*, which it resembles in that in all three species the axilla is dilated laterally and the free portion is distinctly hooked, and the T1–T4 apical fasciae are complete; however, in both *E. attenboroughi* and *E. rufulus* the mandible has a blunt, obtuse preapical tooth, the mesoscutum lacks the distinct paramedian bands present in *E. ainsliei* and is instead largely obscured by pale tomentum, and the preoccipital ridge does not join the hypostomal carina.

**Redescription.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Great Plains to southwestern Ontario (Fig. 5).

**Ecology.** HOST RECORDS: *Epeolus ainsliei* has been collected with possible host species *Colletes susannae* Swenk in Birds Hill Provincial Park (Gibbs et al. 2017) and Spruce Woods Provincial Park (J. Gibbs, personal communication, 2017), Manitoba, Canada and Spring Green Preserve in Sauk County, Wisconsin, USA (Wolf and Ascher 2009). In all cases at least one other species of *Colletes* was observed at the same locality and time as *C. susannae* and *E. ainsliei*, but observations of other *Colletes* were limited to one or two localities.

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Dalea purpurea* Vent. (Leguminosae) and *D. villosa* (Nutt.) Spreng.

**Discussion.** Detailed morphological and taxonomic remarks about this species are given in Onuferko (2017).

**Material studied. Type material.** Primary: USA: **Iowa:** Sioux City, 15.vii.1922, C.N. Ainslie (holotype ♀ [USNM, catalog number: 534035]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACZ1957. Specimens examined and sequenced. Canada: **Manitoba:** 1♀ (PCYU); Birds Hill Provincial Park (50.0190° N; 96.8820° W) (Division 12), 05.viii.2017, J. Gibbs and Nozoe (1♀, JBWM);

**Ontario:** Rondeau Provincial Park (42.2814° N; 81.8427° W) (Beach Access #10, near Visitor Centre), 08.viii.2017, R. Ferrari (1♂, PCYU).

**Non-barcoded material examined.** Canada: **Alberta:** 10♀, 1♂ (BBSL, CNC); **Manitoba:** Yellow Quill Mixed Grass Prairie Preserve (49.6911° N; 99.5747° W) (near Treesbank), 17.vii.2006, A.M. Patenaude (1♀, JBWM); Bald Head Hills (Spruce Woods Provincial Park), 01.viii.1983, W.E. Ralley (1♀, JBWM); Birds Hill Provincial Park (50.0100° N; 96.9100° W) (Division 12), 15.vii.2017, J. Gibbs and Nozoe (1♂, JBWM); Birds Hill Provincial Park (50.0115° N; 96.9065° W) (Division 12), 05.viii.2017, J. Gibbs and Nozoe (2♀, JBWM).

USA: **Colorado:** Longmont (Boulder County), 21.vii.1936, R. Bauer (1♂, CUM); Roggen, 08.vii.1933, M. and H. James and L. Ireland (1♂, CUM); **Iowa:** 1♀ (AMNH); **Michigan:** Edwin S. George Reserve (Livingston County), 12.viii.1960, U.N. Lanham (1♀, CUM); **Minnesota:** 1♀ (EMEC); **Nebraska:** 1♀ (AMNH); **North Dakota:** 7♀, 3♂ (AMNH, EMEC); **Texas:** 3♀, 2♂ (AMNH, CAS, CTMI); **Wyoming:** 1♀ (USNM).

**2. *Epeolus americanus* (Cresson, 1878)**

Figs 6, 7, & 92K

*Phileremus americanus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 83 (♀, ♂); Cresson, 1916. Mem. Am. Entomol. Soc. 1: 111 (♀) [lectotype designation].
*Phileremus montanus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 83 (♂).
*Epeolus lanhami* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 450 (♀).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. americanus* apart from all other North American *Epeolus* except *E. asperatus* and *E. barberiellus*: in females, F2 is not more than 1.1 × as long as wide; the mesoscutum has distinct paramedian bands; the axilla is small to intermediate in size, not extending beyond the midlength of the mesoscutellum and the free portion is less than 1/4 as long as the entire medial length of the axilla, and like the mesoscutellum black; the mesopleuron is closely (i≤1d) and evenly punctate; T1 has a quadrangular discal patch, in dorsal view the longitudinal band is at least as wide as the breadth

of the apical fascia; and the T1 and T2 apical fasciae are interrupted or at least greatly narrowed medially. Whereas in *E. barberiellus* the pronotal lobe and legs, at least from the tibiae to tarsi (sometimes the trochanters and femora as well), are reddish orange, in *E. americanus* the pronotal lobe and legs are brown or black. *Epeolus americanus* is also very similar to *E. asperatus*, but in *E. asperatus* the mesopleuron has much denser punctures ventrolaterally (most i<1d) than that of *E. americanus* and the T3 and T4 fasciae are never complete but broken or at least greatly narrowed laterally, as well as medially into separated or narrowly connected oval patches.

**Redescription.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Widely distributed across Canada and the United States, including Alaska; not known to occur in parts of northeastern North America, the southeastern United States, or the high arctic (Fig. 7).

**Ecology.** See Onuferko (2017) for host and floral records. Floral associations are also indicated in Suppl. material 1, which includes newly discovered associations with *Leucanthemum vulgare* (Vaill.) Lam. (Compositae), *Plagiobothrys* Fisch. & C.A. Mey. (Boraginaceae), *Salix exigua* Nutt. (Salicaceae), and *S. interior* Rowlee based on labels of examined voucher specimens.

**Discussion.** Detailed morphological and taxonomic remarks about this species are given in Onuferko (2017).

**Material studied. Type material.** Primary: USA: **Colorado:** H.K. Morrison (*P. americanus* lectotype ♀ [ANSP, catalog number: 2235]); **Michigan:** Near Saline, 26.vi.1954, U.N. Lanham (*E. lanhami* holotype ♀ [CUM, catalog number: 0000041]); **Nevada:** H. Edwards (*P. montanus* holotype ♂ [ANSP, catalog number: 2231]).

Secondary: USA: **Michigan:** Near Saline, 26.vi.1954, U.N. Lanham (*E. lanhami* allotype ♂ [CUM, catalog number: 0000042]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAB9110.

Specimens examined and sequenced. Canada: **Quebec:** 1♂ (RSKM); **Yukon:** 12♀, 2♂ (PCYU).

USA: **Colorado:** 2♀ (PCYU); **Utah:** 1♀ (BBSL).

**Non-barcoded material examined.** Canada: **Alberta:** 1♂ (CNC); **British Columbia:** 1♀, 2♂ (CNC); **Manitoba:** 1♀ (CNC); Adam Lake (Turtle Mountain Provincial Park), 27.vi.1987, T.D. Galloway (1♀, JBWM); Beaver Creek (Lake Winnipeg), 21.vi.1962, J.A. Garland (1♀, JBWM); **Ontario:** 6♀, 2♂ (CAS, CNC); **Quebec:** 1♀ (USNM); **Saskatchewan:** 2♀ (CNC); **Yukon:** 5♀, 1♂ (PCYU, RSKM).

USA: **Alaska:** 2♀, 3♂ (CNC); **California:** 1♂ (PCYU); 2 mi S Hilmar (Merced County), 14.iv.1961, R.R. Snelling (1♂, LACM); 3 mi SW Ash Creek (Siskiyou County), 16.vi.1974, D. Green (1♀, EMEC); Ash Creek Ranger Station (9 mi E McCloud, Siskiyou County), 07-09.vi.1974, J. Powell (1♂, EMEC), 10-12.vi.1974, R. Coville (4♀, 1♂, EMEC); Hayfork Ranger Station (Trinity County), 19.v.1973, J. Doyen (1♂, EMEC), 23.v.1973, J. Powell (1♀, EMEC); Independence Lake (Sierra County), 24.iv.1974, R.M. Bohart (1♂, UCBME); Lone Pine (Inyo County), 13.v.1969, J.A. Chemsak (1♀, EMEC); Sagehen Creek (Nevada County), 04.vii.??62, R.L. Westcott (1♀, LACM), 01.vii.??70, M.G. Axtman (1♂, LACM), 22.vi.1972, R.M. Bohart (1♀, 1♂, UCBME), 19.vi.1974, R.M. Bohart (4♀, UCBME), 23.vi.1976, N.J. Smith (1♀, UCBME), 23.vi.1976, R.M. Bohart (3♀, 2♂, UCBME), 23.vi.1976, R.M. Giblin (3♀, 1♂, UCBME), 23.vi.1976, R.E. Otondo (1♂, UCBME), 23.vi.1976, G.M. Streett (2♂, UCBME), 23.vi.1976, C.M. Bortfeid (1♂, UCBME), 30.vi.1976, N.J. Smith (1♀, UCBME), 14.vii.1976, R.M. Bohart (1♀, UCBME), 28.vi.1978, D.R. Smart (1♂, UCBME), 28.vi.1978, L.S. Kimsey (2♀, UCBME), 16.vii.1980, R.M. Bohart (1♀, UCBME); **Colorado:** 4♀ (PCYU); vi.1917 (1♀, AMNH); Cirque Meadows (Larimer County), 01.vii.1978, S. Hart (1♂, EMEC); Davenport Camp, 02.vii.1967, F., P., and M. Rindge (1♀, AMNH); Electra Lake, 28.vi.-01.vii.1919 (1♀, AMNH); Longmont (40.1507° N; 105.0385° W) (Weld County), 23.v.2012, V. Scott (1♂, CUM); Near Wolf Creek (37.4999° N; 106.7692° W) (Mineral County), 28.vii.2007, J. Gibbs and C. Sheffield (2♀, PCYU); Ouray (Summit road), 13.vii.1919 (1♂, AMNH); **Idaho:** 1♂ (USNM); **Nevada:** Reno, v.1940, U.N. Lar (1♀, CUM); **Utah:** 2♀ (PCYU); **Virginia:** 1♀ (USNM); **Wyoming:** 13 mi SE Cooke City, 27.vii.1962, F., P., and M. Rindge (1♀, AMNH);

Yellowstone River (between Knowles Falls and Gardiner, Yellowstone National Park), 24.vi.1979, R.E. Dietz (1♂, EMEC).

**3. *Epeolus andriyi* new species**

Figs 8 & 9

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. andriyi* apart from all other North American *Epeolus*: the axilla is large, with the tip extending well beyond the midlength of the mesoscutellum but not as far back as its posterior margin, dilated laterally but relatively straight along the medial margin, and like the mesoscutellum ferruginous; the axilla's free portion is clearly less than 2/5 as long as its entire medial length; the mesopleuron is closely (i≤1d) and evenly punctate; the metasomal terga are black; T1 has a distinct basal fascia, which may be narrowly interrupted medially; the mesoscutum and metasomal terga have bands of bright or pale yellow short appressed setae; at least the T1–T3 apical fasciae are distinctly interrupted medially; and the pseudopygidial area of the female is lunate with the apex <2 × the medial length. *Epeolus andriyi* is most similar to *E. howardi*, but in *E. howardi* the axillae extend further posteriorly, as far back as or beyond the posterior margin of the mesoscutellum, and both the axillae and mesoscutellum are entirely red whereas in *E. andriyi* the mesoscutellum is dark brown or black along the anterior margin. *Epeolus andriyi* is also similar to *E. scutellaris*, but in *E. scutellaris* the T1–T3 apical fasciae are complete or only very narrowly interrupted medially, and the pseudopygidial area of the female is lunate with the apex >2 × the medial length.

**Description.** FEMALE: Length 8.2 mm; head length 1.9 mm; head width 2.6 mm; fore wing length 5.5 mm (margins of both worn in holotype).

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, mesopleuron, and legs. Mandible with apex darker than all but extreme base; preapical tooth lighter than mandibular apex. Antenna brown except scape, pedicel, and F1 extensively orange. F2 with orange spot basally. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum with reddish-brown spot anterolaterally between pronotal lobe and tegula. Wing membrane

dusky subhyaline, slightly darker at apex. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, except beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum sparser medially, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally by few sparsely scattered pale hairs. T1–T3 with apical fasciae interrupted medially and narrowed before becoming somewhat broader laterally; T2 with fascia without anterolateral extensions of tomentum, although few sparsely scattered pale hairs present. T4 with fascia narrowed medially. T5 with two patches of pale tomentum (both quite faint in holotype because much of pubescence discolored or rubbed off) lateral to and contacting pseudopygidial area. T5 with pseudopygidial area lunate, its apex less than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate matte spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d), the interspaces shining; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc; the interspaces shining somewhat.

*Structure.* Preapical tooth inconspicuous, blunt and obtuse. Labrum with pair of small subapical denticles, each preceded by small discrete longitudinal ridge. Frontal keel not strongly raised. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.5). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum weakly bigibbous. Axilla large, its lateral margin (L) half as long as mesoscutellar width (W) (L/W ratio = 0.5) and tip extending well beyond midlength of mesoscutellum but not as far back as its posterior margin; axilla with tip

clearly visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, not noticeably longer than wide (L/W ratio = 1.1); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

**Etymology.** This species is named in honor of my father, Rev. Andriy Onuferko, in gratitude for encouraging my interests in the natural world and for his assistance in collecting *Epeolus* in the field.

**Distribution:** Presently known from a single location along the Patuxent River in Maryland, USA (Fig. 9).

**Ecology.** HOST RECORDS: The host species of *E. andriyi* is/are presently unknown.

FLORAL RECORDS: Unknown.

**Discussion.** *Epeolus andriyi* and *E. howardi* are very similar to one another, and both species have been collected in Maryland, USA in late August. Although *E. andriyi* is known from only two specimens, in both the axillae are shorter than in any examined specimen of *E. howardi*. The status of *E. andriyi* as a separate species is further supported by a separate BIN, but unusually its nearest neighbor is *E. lectoides*, from which *E. andriyi* exhibits a large barcode sequence divergence (7.1%).

**Material studied. Type material.** Primary: USA: **Maryland:** Jug Bay Wetlands Sanctuary (38.7839° N; 76.7014° W) (Anne Arundel County), 31.viii.2004, B. Hollister (♀ holotype [04-MD-1692], RSKM).

Secondary: USA: **Maryland:** Jug Bay Wetlands Sanctuary (38.7839° N; 76.7014° W) (Anne Arundel County), 31.viii.2004, B. Hollister (♂ allotype [04-MD-1691], RSKM).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAX7179. See Type material for specimens examined and sequenced (indicated by unique identifier number in square brackets).

**4. *Epeolus asperatus* Cockerell, 1909**

Figs 2D, 10, 11, & 92L

*Epeolus asperatus* Cockerell, 1909. Ann. Mag. Nat. Hist. 5: 25 (♀).
*Epeolus melectimimus* Cockerell & Sandhouse, 1924. Proc. Calif. Acad. Sci. (4) 13: 317 (♂), **syn. n.**

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. asperatus* apart from all other North American *Epeolus* except *E. americanus* and *E. barberiellus*: in females, F2 is not more than 1.1 × as long as wide; the mesoscutum has distinct paramedian bands; the axilla is small to intermediate in size, not extending beyond the midlength of the mesoscutellum and the free portion is less than 1/4 as long as the entire medial length of the axilla, and like the mesoscutellum black; the mesopleuron is closely (most i<1d) and evenly punctate; T1 has a quadrangular discal patch, in dorsal view the longitudinal band is at least as wide as the breadth of the apical fascia; and the T1 and T2 apical fasciae are interrupted or at least greatly narrowed medially. Whereas in *E. barberiellus* the legs, at least from the tibiae to tarsi (sometimes the trochanters and femora as well), are reddish orange and the metasomal terga are fasciate, in *E. asperatus* the legs are brown or black and the T3 and T4 fasciae are broken or at least greatly narrowed laterally, as well as medially into separated or narrowly connected oval patches. *Epeolus asperatus* is most similar to *E. americanus*, but in *E. americanus* the mesopleuron has sparser punctures ventrolaterally (i≤1d) than that of *E. asperatus*, with the interspaces shining, and the T3 and T4 fasciae are complete or broken medially and/or laterally, but rarely into separated oval patches.

**Redescription.** FEMALE: Length 7.8 mm; head length 2.0 mm; head width 2.8 mm; fore wing length 5.4 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, and legs. Mandible with apex darker than rest of mandible; preapical tooth lighter than mandibular apex (difficult to see in the *E. asperatus* holotype; described from non-type specimens). Antenna brown except F1 and F2 orange in part. Flagellum slightly lighter than conspicuously dark brown scape and pedicel, primarily due to extensive pilosity on flagellum. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs with brown or black more extensive than reddish orange.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, ventrolateral half nearly bare. Metanotum with tomentum rubbed off medially in the *E. asperatus* holotype, but somewhat sparser medially and uniformly off white in non-type specimens. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex, and narrow, such that longitudinal band nearly half as wide as width of discal patch in dorsal view. T2–T4 with fasciae interrupted medially and with anterolateral extensions of sparser tomentum. T3 and T4 with fasciae also interrupted laterally, appearing as pair of oval patches between medial and lateral interruptions. T5 with two patches of pale tomentum lateral to and separate from pseudopygidial area (difficult to see in the *E. asperatus* holotype because T5 mostly retracted; described from non-type specimens). T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate (i<1d). Mesopleuron with ventrolateral half densely punctate (i<1d); mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth with blunt tip. Labrum with pair of small subapical denticles, each preceded by small discrete longitudinal ridge. Frontal keel not strongly raised. Scape with

greatest length 1.9 × greatest width. F2 as long as wide (L/W ratio = 1.0). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5–2 MOD at its terminal (difficult to see in the *E. asperatus* holotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin (L) less than half as long as mesoscutellar width (W) (L/W ratio = 0.4) and tip not extending beyond midlength of mesoscutellum; axilla with tip visible, but unattached to mesoscutellum for less than 1/3 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore wing with second submarginal crossvein incomplete in the *E. asperatus* holotype; with submarginal cells two or three and closed or second submarginal crossvein incomplete in non-type specimens. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, nearly as long as wide (L/W ratio = 0.8); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate V-shaped but apically rounded, with large deep, well-separated punctures, with the interspaces shining.

**Distribution:** Central and southern California (Fig. 11).

**Ecology.** HOST RECORDS: I have collected nine representatives of this species at the Robert J. Bernard Biological Field Station in Claremont, California, USA in the spring of 2016 (see Material studied), and the only *Colletes* collected or observed was a single female of a predominantly black species with pale pubescence limited to the mesosoma. The collected female of the possible host species was barcoded, and using Stephen's (1954) key identified as *C. californicus* Provancher. However, its sequence clusters with sequences of specimens collected in New Mexico (also in the spring of 2016) and identified as *C. sphaeralceae* Timberlake (with entirely/predominantly pale pubescence) through the use of Stephen's (1954) key, dissection of the male terminalia, and collection from red *Sphaeralcea* A. St.-Hil. (Malvaceae) flowers, and all were assigned the same BIN (BOLD:ABZ4529). Another predominantly black female specimen from the San Diego National Wildlife Refuge Otay-Sweetwater Unit in California was barcoded (its image and 601 bp sequence are available on the Barcode of Life Data Systems website [http://www.barcodinglife.org/]), and was assigned the same BIN as the female from Claremont and specimens from New Mexico.

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Lasthenia* Cass. (Compositae) and *Plagiobothrys*.

**Discussion.** Brumley (1965) synonymized *E. asperatus* and *E. melectimimus* under *E. americanus*, but current evidence suggests that the holotypes of *E. asperatus* and *E. melectimimus* belong to a cryptic species within the "*americanus* group", distinct from *E. americanus* and *E. barberiellus*. In addition to the subtle diagnostic morphological features that separate *E. asperatus* from *E. americanus* and *E. barberiellus*, the status of *E. asperatus* as a separate species is supported by a separate BIN and large barcode sequence divergence (4.4%) from its nearest neighbor, *E. barberiellus*.

*Epeolus melectimimus*, with three submarginal cells, was described by Cockerell and Sandhouse (1924), who claimed that the species resembles a small *Pseudomelecta* Radoszkowski (a subgenus of *Melecta* Latreille in Michener 2007), from which it can be readily distinguished based on differences in the marginal cell. In the *E. asperatus* holotype, the second submarginal crossvein on each side is incomplete and inconspicuous. A series of *E. asperatus* was collected from the Robert J. Bernard Biological Field Station in Claremont, California, USA, which is in the same county as the type locality (Los Angeles). In some specimens, the fore wing has three submarginal cells whereas in others, the second submarginal crossvein is incomplete or lacking entirely. In some specimens, one fore wing has three submarginal cells and the other has an incomplete second submarginal crossvein. The male holotype of *E. melectimimus* was examined, and excluding sex-specific features the specimen with few exceptions agrees with the present redescription based on the female holotype of *E. asperatus*. Along with the abovementioned differences in wing venation, the pronotal lobe and tegula are darker in the holotype of *E. melectimimus* than in that of *E. asperatus*, but these differences fall within the range of observed intraspecific morphological variation among sequenced specimens. Although both *E. americanus* and *E. asperatus* are present in California, *E. americanus* appears to be absent from the southern part of the state.

**Material studied. Type material.** Primary: USA: **California:** Huntington Lake (Fresno County), 07.vii.1919, E.P. Van Duzee (*E. melectimimus* holotype ♂ [CAS, catalog number:

01612]); Los Angeles (Los Angeles County), 24.iv.1909, F. Grinnell, Jr. (*E. asperatus* holotype ♀ [USNM, catalog number: 534036]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACZ2142. Specimens examined and sequenced. USA: **California:** Robert J. Bernard Biological Field Station (Claremont, Los Angeles County), 18.iv.2002, M.G. Rightmyer (1♀, KUNHM); Robert J. Bernard Biological Field Station (34.1083° N; 117.7100° W) (Claremont, Los Angeles County), 13.iv.2016, T.M. Onuferko (2♂, PCYU).

**Non-barcoded material examined.** USA: **California:** 2 mi S Hilmar (Merced County), 19.iv.1960, R.R. Snelling (1♀, AMNH); 2 mi S Pearblossom (Los Angeles County), 01-02.v.1977, R.R. Snelling (1♂, LACM); Arroyo Seco Campground (Monterey County), 01.v.1960, F.D. Parker (1♂, UCBME), 19.v.1964, R.M. Bohart (1♂, UCBME), 11.v.1971, R.M. Bohart (3♀, 2♂, UCBME); Claremont (Los Angeles County), Baker (1♂, USNM), Metz (1♀, AMNH); Devore (San Bernardino County), 21.vi.1974, J.C. and E.M. Hall (1♂, UCR); East Fork Kaweah River (Tulare County), 02.vii.1976, T.L. Griswold (1♀, BBSL); Millard Canyon (Riverside County), 07.iv.1974, J.C. and E.M. Hall (1♀, UCR); Moreno Valley (base of Box Springs Mountains, Riverside County), 26.iv.1992, R.K. Velten (1♀, UCR); Robert J. Bernard Biological Field Station (34.1083° N; 117.7100° W) (Claremont, Los Angeles County), 13.iv.2016, T.M. Onuferko (2♀, 1♂, PCYU), 14.iv.2016, T.M. Onuferko (1♀, PCYU), 26.iv.2016, T.M. Onuferko (3♂, PCYU); W L Jepson Prairie Preserve (TNC) (13 mi S Dixon, Solano County), 20.v.1983, J.D. Barbour (1♂, UCBME).

**5. *Epeolus attenboroughi* new species**

Figs 3B, 12, 13, 94B, 95B, & 96A

**Diagnosis.** The following morphological features in combination can be used to tell *E. attenboroughi* apart from all other North American *Epeolus* except *E. rufulus*: the mandible has a blunt, obtuse preapical tooth; the preoccipital ridge does not join the hypostomal carina; the mesoscutum is largely obscured by pale tomentum; the axilla is elongate, extending well beyond the midlength of the mesoscutellum but not as far back as its posterior margin, and the free

portion is distinctly hooked; the mesopleuron is closely (most i<1d) and evenly punctate; and T1–T4 have complete apical fasciae. Whereas in *E. rufulus* the discal patch is so wide that the longitudinal band is barely visible in dorsal view and in females F2 is noticeably longer than wide, in *E. attenboroughi* T1 has a comparatively narrow discal patch (the longitudinal band is more than half as wide as the breadth of the apical fascia in dorsal view) and in females F2 is less than 1.2 × as long as wide. *Epeolus attenboroughi* is also similar to *E. ainsliei* in that in both species the axilla is dilated laterally and the free portion is distinctly hooked, and the T1–T4 apical fasciae are complete; however, in *E. ainsliei* the mandible is simple, the preoccipital ridge joins the hypostomal carina, and the mesoscutum has distinct paramedian bands.

**Description.** FEMALE: Length 6.8 mm; head length 1.7 mm; head width 2.2 mm; fore wing length 4.5 mm.

*Integument coloration*. Black in part, at least partially ferruginous on mandible, labrum, clypeus, antenna, pronotal lobe, tegula, axilla, mesopleuron, legs, metasomal terga (including pygidial plate), and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth slightly lighter than mandibular apex. Antenna brown and orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs entirely reddish orange.

*Pubescence*. Face with tomentum densest around antennal socket, slightly sparser on clypeus, upper paraocular and frontal areas, and vertexal area. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum, mesoscutellum, and axilla largely obscured by pale tomentum. Mesopleuron densely hairy, except for sparsely hairy circular patch occupying much of ventrolateral half of mesopleuron. Metanotum with tomentum uninterrupted, uniformly off white. T1 with median quadrangular reddish-brown discal patch entirely enclosed by pale tomentum and narrow, such that longitudinal band more than half as wide as breadth of apical fascia in dorsal view. T2–T4 with fasciae complete, T2 with fascia with anterolateral extensions of sparser tomentum. T5 with two patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~1/3 MOD.

*Surface sculpture*. Punctures dense. Labrum and clypeus with punctures equally dense (i<1d). Impunctate spot lateral to lateral ocellus absent. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate (i<1d). Mesopleuron with ventrolateral half densely punctate (i<1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure*. Preapical tooth blunt and obtuse. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.7 × greatest width. F2 not noticeably longer than wide (L/W ratio = 1.1). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum weakly bigibbous. Axilla large, its lateral margin (L) more than half as long as mesoscutellar width (W) (L/W ratio = 0.6) and tip extending well beyond midlength of mesoscutellum but not as far back as its posterior margin; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion approximately half its medial length; axilla with lateral margin arcuate and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, as long as wide (L/W ratio = 1.0); mesopleuron almost entirely obscured by white tomentum; S4 and S5 with much longer coppery to silvery subapical hairs, which individually are often darker apically; pygidial plate apically rounded, with large deep, well-separated punctures, with the interspaces shining.

**Etymology.** This species is named in honor of English broadcaster and naturalist Sir David Attenborough in recognition of his inspiring books and television programs on natural history.

**Distribution:** New Mexico and southern Colorado (Fig. 13).

**Ecology.** HOST RECORDS: The host species of *E. attenboroughi* is/are presently unknown.

FLORAL RECORDS: Unknown.

**Discussion.** *Epeolus attenboroughi* is similar in overall appearance to *E. ainsliei* and *E. rufulus*, and the ranges of the three species overlap to some extent. Although BIN-compliant sequences are presently not available for *E. attenboroughi*, partial sequences 421 bp and 289 bp in length are available for two specimens (male and female respectively) collected at the same locality and within one day of each other, and there is virtually no divergence (<1%) between the two. Moreover, the 421 bp sequence does not cluster closely with any sequences from other *Epeolus* species in a NJ tree of sequences >300 bp in length (Suppl. material 2). The longer of the two partial sequences is most similar (95.2%) to sequences from *E. glabratus* and *E. lectoides* (very different species).

In general, there is little morphological variation among examined specimens except in integument coloration; the axillae and mesoscutellum range from entirely black to partially ferruginous. Based on known records, adults of *E. attenboroughi* are active in summer.

**Material studied. Type material.** Primary: USA: **Colorado:** Great Sand Dunes National Monument (Alamosa County), 03-13.vii.1989, W.J. Bell (holotype ♀, KUNHM).

Secondary: USA: **Colorado:** Great Sand Dunes National Monument (Alamosa County), 10.vii.1991, B. Cutler (paratype ♀, KUNHM), 03-13.vii.1989, W.J. Bell (paratypes 1♀, 1♂, KUNHM), 11.vii.1991, B. Alexander and B. Cutler (allotype ♂, KUNHM), 11.vii.1991, B. Alexander and B. Cutler (paratypes 3♂, KUNHM); **New Mexico:** 24 km W Quemado (Catron County), 02.ix.1990, T.L. Griswold (paratype ♀, BBSL).

**DNA barcoded material with BIN-compliant sequences.** Unavailable.

**6. *Epeolus australis* Mitchell, 1962**

Figs 2A, 14, 15, 97I, & 103A

*Epeolus australis* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 441 (♀).

**Diagnosis.** The following morphological features in combination can be used to tell *E. australis* apart from all other North American *Epeolus*: the frontal carina is strongly convex, such that the supraclypeal area is distinctly protuberant in lateral view; T1–T4 have complete fasciae; and the

T2 fascia has a pair of anterolateral extensions of tomentum that are strongly convergent basally. In *E. chamaesarachae* and *E. diadematus* and commonly in *E. bifasciatus* the frontal carina is also strongly convex, but in the first two species the vertexal area has two pairs of shiny (usually impunctate) protrusions and in *E. bifasciatus* the frontal area bears a pair of granulose protrusions whereas in *E. australis* the frontal and vertexal areas lack protrusions. *Epeolus australis* most closely resembles *E. brumleyi*, but in *E. brumleyi* the frontal carina is only weakly convex and the pygidial plate of the male is wider (the medial length ≈ the basal width) than in *E. australis* (the medial length is ~1.5 × the basal width).

**Redescription.** FEMALE: Length 7.5 mm; head length 2.0 mm; head width 2.8 mm; fore wing length 5.7 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, mesoscutellum, legs, pygidial plate, and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth slightly lighter than mandibular apex. Both antennae missing in holotype, but brown and orange in part in paratype. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket, slightly sparser on clypeus, upper paraocular and frontal areas, and vertexal area. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron with upper half densely hairy, except beneath base of fore wing (hypoepimeral area); ventrolateral half sparsely hairy. Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch elliptical and very wide, the basal and apical fasciae only narrowly joined laterally. T1 with basal and apical fasciae and T2–T4 with apical fasciae complete, T2 with fascia with basomedially convergent anterolateral extensions of tomentum. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area, enclosing pseudopygidial area in triangle, except for medial separation at base. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~1/3 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger punctures than clypeus, but punctures of both equally dense (i≤1d). Impunctate spot lateral to lateral ocellus absent in holotype, but shiny spot present in some non-type specimens. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i<1d); mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth inconspicuous, blunt and obtuse. Labrum with pair of small subapical denticles (approximately at 1/4 length of labrum from apical margin) not preceded by carinae. Frontal keel strongly raised. Scape (missing in holotype) with greatest length 1.6 × greatest width in paratype. F2 (missing in holotype) not noticeably longer than wide (L/W ratio = 1.1) in paratype. Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin (L) nearly half as long as mesoscutellar width (W) (L/W ratio = 0.4–0.5) and tip not extending beyond midlength of mesoscutellum; axilla with tip visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, as long as wide (L/W ratio = 1.0); S4 and S5 with much longer coppery to silvery subapical hairs, which individually are often darker apically; pygidial plate unusually narrow (*Triepeolus*-like) and apically rounded, with large deep punctures closely clustered.

**Distribution:** Mid-Atlantic states to Texas and presumably Mexico, given the close proximity of some collection localities (e.g., Eagle Pass, Texas) to the Mexico–United States border (Fig. 15).

**Ecology.** HOST RECORDS: The host species of *E. australis* is/are presently unknown.

FLORAL RECORDS: Mitchell (1962) indicated floral associations with *Ceanothus* L. (Rhamnaceae), *Rubus* L. (Rosaceae), *Senecio* L. (Compositae), and *Specularia* (now *Triodanis*? Raf. ex Greene) (Campanulaceae). Labels of examined voucher specimens further indicate

associations with *Chaetopappa asteroides* (Nutt.) Nutt. ex DC. (Compositae), *Hymenopappus artemisiifolius* DC. (Compositae), and *Sphaeralcea*.

**Discussion.** This southeastern species displays minor sexual dimorphism in the coloration of the mesoscutellum, which is bright ferruginous in females and dark ferruginous to black in males. Otherwise, there is very little morphological variation among examined specimens. Although BIN-compliant sequences are presently not available for *E. australis*, 422 bp sequences were obtained from two male specimens (one from New Jersey, USA and one from South Carolina, USA), and there is virtually no divergence (<1%) between the two. Moreover, these sequences do not cluster with any sequences from other *Epeolus* species in a NJ tree (Suppl. material 2). Based on known records, adults of *E. australis* are active in spring.

**Material studied. Type material.** Primary: USA: **North Carolina:** Raleigh, 19.v.1950, T.B. Mitchell (holotype ♀, NCSU).

Secondary: USA: **North Carolina:** Raleigh, 09.v.1948, T.B. Mitchell (paratype ♀, NHMUK), 19.v.1950, T.B. Mitchell (paratype ♀, USNM).

**DNA barcoded material with BIN-compliant sequences.** Unavailable.

**Non-barcoded material examined.** USA: **Florida:** Alachua (Alachua County), 29.iv.1974, E.E. Grissell (2♀, UCBME); **Georgia:** Augusta (Richmond County), 18.v.1959, R.R. Snelling (1♀, LACM), 17.v.1959, R.R. Snelling (1♀, LACM), 03.v.1959, R.R. Snelling (1♂, LACM), 26.iv.1959, R.R. Snelling (1♂, LACM); Fort Gordon (Richmond County), 08.v.1958, R.R. Snelling (1♀, LACM); **Maryland:** Bowie (Prince George's County), 08.vi.1968, R.R. Snelling (1♂, LACM); **New Jersey:** Forsythe (39.5296° N; 74.3421° W) (Atlantic and Ocean counties), 01-30.vi.2008, M. Springer (1♀, BIML); **South Carolina:** Carolina Sandhills National Wildlife Refuge (34.6043° N; 80.2469° W) (Chesterfield County), 18-19.v.2006, S.W. Droege (1♂, BIML); **Texas:** 10.7 mi S Dryden (Terrell County), 21.iv.1973, R.R. Snelling (1♂, LACM); 12 mi S Seguin (29.4060° N; 97.8550° W) (TX-123, Guadalupe County), 03.v.2014, J.L. Neff (1♀, CTMI); 8-25 km N Castroville (Medina County), 12.v.1988, B.N. Danforth (1♀, KUNHM); Camp Swift (30.2910° N; 97.3060° W) (Bastrop County), 24.iv.2003, J.L. Neff (1♀, CTMI);

Eagle Pass (Maverick County), 28.iii.1946, C.D. Michener (2♂, AMNH); Hwy 83 (14 mi S Jct. Texas State Hwy 44, Webb County), 21.iv.1973, R.R. Snelling (1♀, LACM); Nacogdoches (Nacogdoches County), 14.iv.1960 (1♀, KUNHM); Stengl Lost Pines Research Station (30.0800° N; 97.1830° W) (Bastrop County), 02.iv.2006, J.L. Neff (1♀, CTMI).

**7. *Epeolus autumnalis* Robertson, 1902**

Figs 16 & 17

*Epeolus autumnalis* Robertson, 1902. Entomol. News 13: 81 (♀, ♂). Webb, 1980. Ill. Nat. Hist. Surv. Bull. 32: 108 (♀) [lectotype designation (by W.E. LaBerge)].

**Diagnosis.** The following morphological features in combination can be used to tell *E. autumnalis* apart from all other North American *Epeolus*: the axilla is large, with the tip extending well beyond the midlength of the mesoscutellum but not as far back as its posterior margin, dilated laterally, and like the mesoscutellum black; the mesopleuron is closely (i≤1d) and evenly punctate; the T1 discal patch is so wide that the longitudinal band is barely visible in dorsal view; and the T2 fascia lacks lobe-like anterolateral extensions of tomentum, although a few sparsely scattered pale hairs are sometimes present. *Epeolus autumnalis* is similar to *E. scutellaris* in terms of surface sculpture and the patterns of pubescence on the mesosoma and metasoma, but in *E. scutellaris* at least the axilla is partially to entirely ferruginous (as is often the mesoscutellum), and the axilla is more elongate, extending to or beyond the band of pale tomentum along the posterior margin of the mesoscutellum.

**Redescription.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Eastern North America (Fig. 17).

**Ecology.** See Onuferko (2017) for host and floral records. Floral associations are also indicated in Suppl. material 1.

**Discussion.** Detailed morphological and taxonomic remarks about this species are given in Onuferko (2017).

**Material studied. Type material.** Primary: USA: **Illinois:** Carlinville (Macoupin County), C.A. Robertson (lectotype ♀ [INHS, catalog number: 44381]).

Secondary: USA: **Illinois:** Carlinville (Macoupin County), C.A. Robertson (lectoallotype ♂ [INHS, catalog number: 44382]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAF2361. Specimens examined and sequenced. Canada: **Nova Scotia:** 2♀, 1♂ (PCYU, RSKM); **Ontario:** 1♀ (PCYU).

USA: **New York:** 1♀ (AMNH).

**Non-barcoded material examined.** Canada: **Nova Scotia:** 2♀ (PCYU, RSKM); Avonport (45.1189° N; 64.2634° W) (Kings County), 27.viii.2000, C. Sheffield (1♂, PCYU); **Ontario:** 14♀, 24♂ (DEBU, PCYU, ROM); King (44.0410° N; 79.5060° W), 23.viii.2000, V. Kushnir (1♂, PCYU); King (44.0430° N; 79.3100° W), 28.viii.2002, V. Kushnir (1♂, PCYU); King (44.0430° N; 79.5410° W), 06.ix.2003, J. Grixti (1♂, PCYU).

USA: **Maryland:** 2♂ (BIML); **Massachusetts:** 1♀, 2♂ (AMNH, BIML); **New York:** 1♀, 1♂ (AMNH, CAS); Lime Hollow (42.5650° N; 76.2550° W) (Cortland County), 03.ix.2011, J. Gibbs (1♂, JBWM); **Virginia:** Glencarlyn, 06.ix.???? (1♂, CUM).

**8. *Epeolus axillaris* new species**

Figs 18, 19, & 94A

*Epeolus scopulus* Brumley, 1965. M.S. thesis, Utah State University, Logan 66 (♀) [*nomen nudum*].

**Diagnosis.** *Epeolus axillaris* can be differentiated from all other *Epeolus* species in North America by the distinct posteromedial depression of the metanotum; in all other species the metanotum is flat, strongly convex, or weakly convex. *Epeolus axillaris* closely resembles *E.*

*banksi*, *E. minimus*, and *E. olympiellus* in that the axilla (except sometimes the tip) and mesoscutellum are black; T1 has a quadrangular discal patch, in dorsal view the longitudinal band is at least half as wide as the breadth of the apical fascia; and the T2 fascia has lobe-like anterolateral extensions of tomentum. However, in all three species the metanotum is flat and the axilla does not extent much beyond the midlength of the mesoscutellum, whereas in *E. axillaris* the axilla is more elongate, extending well beyond the midlength of the mesoscutellum but not as far back as its posterior margin.

**Description.** FEMALE: Length 10.0 mm; head length 2.1 mm; head width 2.9 mm; fore wing length 6.9 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, legs, T5, and pygidial plate. Mandible with apex darker than all but extreme base; preapical tooth slightly lighter than mandibular apex (difficult to see in holotype because mandible closed; described from paratypes). Flagellum brown and (except F1) slightly lighter than partially dark brown (otherwise orange) scape, pedicel, and F1, primarily due to extensive pilosity on flagellum. Axilla only with tip orange. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs, except reddish-orange mesotibia, metatibia, and tarsi, with brown or black more extensive than reddish orange.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band wider and joined posteriorly. Mesopleuron densely hairy, except for two sparsely hairy circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted except for median bare patch in posterior half, uniformly off white. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2–T4 with fasciae interrupted medially and narrowed before becoming somewhat broader laterally, T2 with fascia with anterolateral extensions of equally dense tomentum. T5 with two patches of pale tomentum bordering and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on impressed disc of

apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~2/5 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron largely obscured by tomentum, but ventrolateral half densely punctate (i<1d) to rugose where exposed; mesopleuron with punctures more or less equally dense throughout where exposed. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labrum with pair of small subapical denticles, each preceded by small discrete longitudinal ridge. Frontal keel not strongly raised. Scape with greatest length 1.7 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5–2 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla large, its lateral margin (L) half as long as mesoscutellar width (W) (L/W ratio = 0.5) and tip extending well beyond midlength of mesoscutellum but not as far back as its posterior margin; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Metanotum with posteromedial depression beneath overhanging anterior portion. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, not noticeably longer than wide (L/W ratio = 1.1); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

**Etymology.** The name is in reference to the axillae of this species, which are distinctly longer than those of the similar *E. minimus* and *E. olympiellus*.

**Distribution:** California and western Nevada. According to Brumley (1965), this species also ranges into Oregon, but its presence in that state could not be verified in the present study (Fig. 19).

**Ecology.** HOST RECORDS: The host species of *E. axillaris* is/are presently unknown.

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Chrysothamnus* Nutt. (Compositae) (possibly in reference to plants that now are in the genus *Ericameria* Nutt. (Compositae)), *Ericameria nauseosa* var. *nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird, *E. nauseosa* var. *oreophila* (A. Nelson) G.L. Nesom & Baird, and *E. parryi* (A. Gray) G.L. Nesom & Baird.

**Discussion.** This species is most similar to *E. minimus* and *E. olympiellus*, and there is overlap in the ranges of all three species. Brumley (1965) recognized *E. axillaris* as a separate species in which the axilla is more elongate and the metanotum is uniquely depressed posteromedially. The morphological distinction is supported by molecular data, as sequenced specimens exhibiting these attributes were assigned a separate BIN from either of the other two species.

**Material studied. Type material.** Primary: USA: **Nevada:** Cottonwood Creek (38.6013° N; 118.8280° W) (Mineral County), 14.viii.1998, F.D. Parker (holotype ♀ [CCDB-28237 D01], BBSL).

Secondary: USA: **California:** Antioch (Contra Costa County), x.1938, J.A. Downes (paratype ♂, CNC), 10.ix.1947, P.D. Hurd (paratype ♂, BBSL), 10.ix.1947, U.N. Lanham (paratype ♀, CUM); Bodie (Mono County), 21.ix.1958, A.S. Menke and L.A. Stange (paratype ♀, LACM); Hot Creek (Mono County), 29.viii.1969, E.E. Grissell (paratypes 3♀, UCBME), 29.viii.1969, R.M. Bohart (paratype ♂, UCBME); Parker Creek at Walker Lake Road (37.8768° N; 119.1203° W) (Mono County), 02.ix.2009, G.R. Ballmer (allotype ♂ [CCDB-28313 H10], UCR), 02.ix.2009, G.R. Ballmer (paratypes 2♂ (1 barcoded [CCDB-28313 H08]), UCR); Upper Santa Ana River (San Bernardino County), 22.ix.1946, G.H. and J.L. Sperry (paratype ♂, KUNHM); **Nevada:** 17 mi N Sparks (Washoe County), 02.ix.1957, E.G. Linsley (paratype ♀, BBSL), 02.ix.1957, E.G. Linsley (paratype ♀, USNM); 3 mi N Minden (Douglas County), 10.ix.1957, R.C. Bechtel (paratype ♀, AMNH); Reno, 09.ix.1961, F.D. Parker (paratype ♂, UCBME).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACZ2412. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**9. *Epeolus banksi* (Cockerell, 1907)**

Figs 20, 21, & 96F

*Triepeolus banksi* Cockerell, 1907a. Entomologist 40: 135 (♂).
*Epeolus banksi* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 442.

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. banksi* apart from all other North American *Epeolus* except *E. minimus* and *E. olympiellus*: in females, F2 is at least 1.2 × as long as wide; the mesoscutum has distinct paramedian bands; the axilla is small to intermediate in size, not extending much beyond the midlength of the mesoscutellum (extending to <2/3 its length) but the free portion is more than 1/4 as long as the entire medial length of the axilla, and the axilla and mesoscutellum are black; the mesopleuron is closely (most i<1d) and evenly punctate; T1 has a quadrangular discal patch, in dorsal view the longitudinal band is at least half as wide as the breadth of the apical fascia; and the T2 fascia has anterolateral extensions of tomentum. Whereas in *E. minimus* and *E. olympiellus* the mesoscutum and metasomal terga have bands of off-white to pale yellow short appressed setae, in *E. banksi* the mesoscutum and metasomal terga have bands of gray short appressed setae. In *E. banksi*, the integument is entirely dark brown or black. In *E. olympiellus*, at least the pronotal lobe is ferruginous. In *E. minimus* from California, the integument is often entirely dark brown or black, but throughout most of its range *E. minimus* exhibits reddish-orange coloration on the labrum, antenna, pronotal lobe, and/or legs, except foreleg, from trochanters to tarsi. Both sexes of *E. banksi* are larger (~10 mm in length) on average than *E. minimus* or *E. olympiellus* (7–8 mm in length).

**Redescription.** MALE: Length 9.4 mm; head length 2.3 mm; head width 3.3 mm; fore wing length 7.5 mm.

*Integument coloration*. Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, tegula, and legs. Mandible black except apex reddish brown; preapical tooth same color as mandibular apex (difficult to see in holotype; described from non-type specimens). Flagellum, except right F1 and F2, missing in holotype, but brown and (except F1) slightly lighter than conspicuously dark brown scape and pedicel, primarily due to extensive pilosity on flagellum, in non-type specimens. Wing membrane subhyaline, apically dusky. Legs, except reddish-orange tarsi, with brown or black more extensive than reddish orange.

*Pubescence*. Face with tomentum densest on clypeus and around antennal socket, sparser on upper paraocular area and vertexal area. Dorsum of mesosoma and metasoma with bands of off-white to pale gray short appressed setae. Mesoscutum with paramedian band. Mesopleuron densely hairy, except for two sparsely hairy circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted, uniformly off white. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2–T6 with fasciae interrupted medially, those of T2–T4 narrowed before becoming somewhat broader laterally, T2 with fascia with anterolateral extensions of sparser tomentum. S4 and S5 with long coppery to silvery subapical hairs, which individually are often darker apically.

*Surface sculpture*. Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate matte spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i<1d); mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure*. Labral apex with pair of small denticles, each preceded by longitudinal carina. Frontal keel not strongly raised. Scape with greatest length 1.6 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.2). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5–2 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin (L) nearly half as long as mesoscutellar width (W) (L/W ratio = 0.4–0.5) and tip not extending much beyond midlength of mesoscutellum (extending to <2/3 its length); axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore

wing with three submarginal cells. Pygidial plate apically rounded, with large deep punctures closely clustered.

FEMALE: Description as for male except for usual secondary sexual characters and as follows: F2 even longer than wide (L/W ratio = 1.4); T5 with two patches of pale tomentum bordering and separate from pseudopygidial area present only in female; T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on flat disc of apicomedial region elevated from rest of tergum; S4 and S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~2/5 MOD); pygidial plate apically truncate, with small, denser punctures.

**Distribution:** Maryland to North Carolina (Fig. 21).

**Ecology.** HOST RECORDS: The host species of *E. banksi* is/are presently unknown.

FLORAL RECORDS: Mitchell (1962) indicated a floral association with *Fragaria* L. (Rosaceae). Labels of examined voucher specimens further indicate associations with *Solidago* L. (Compositae) and *Symphyotrichum ericoides* (L.) G.L. Nesom (Compositae).

**Discussion.** Most of the specimens of this species that were examined were collected in the Washington metropolitan area. While Mitchell (1962) indicated *Epeolus banksi* as being quite prevalent across the Eastern United States, reportedly ranging from Minnesota to New Jersey and North Carolina, it seems that the name has been commonly misapplied to specimens of *E. minimus* (as in MacKay and Knerer (1979) for example, and probably by Mitchell (1962) as well). *Epeolus banksi* is much larger than *E. minimus*, and has completely black integument, but unlike similarly dark specimens of *E. minimus* from California, *E. banksi* has gray as opposed to pale yellow bands of tomentum on the mesosoma and metasoma. Unfortunately, no recently collected material was available for barcode sequencing, and the specimens seen are all from the early 1900s. The absence of this species from recent collections has not gone unnoticed (e.g in Colla et al. 2012 it is listed among the bee species not collected since 1990). Increased urbanization in and around Washington D.C. may have resulted in the extirpation of this species there, and perhaps it has even disappeared entirely throughout its earlier range. Hence, extensive efforts should be made to rediscover this species, by sampling its apparent historical range

between North Carolina and Maryland, to assess its conservation status. The flight season of *E. banksi* appears to be late summer/early autumn.

**Material studied. Type material.** Primary: USA: **Virginia:** Falls Church, 26.viii.????, N. Banks (holotype ♂ [USNM, catalog number: 534038]).

Secondary: USA: **Virginia:** Falls Church, 07.ix.????, N. Banks (paratype ♂, CAS).

**DNA barcoded material with BIN-compliant sequences.** Unavailable.

**Non-barcoded material examined.** USA: **Maryland:** Glen Echo (Montgomery County), 30.viii.1923, J.R. Malloch (1♂, USNM); **North Carolina:** Valley of Black Mountains, 30.ix.1906, W. Beutenmuller (1♂, AMNH); **Virginia:** Chain Bridge, 10.ix.1922, J.R. Malloch (1♂, USNM); Falls Church, G.G. Rohwer (1♂, USNM); Glencarlyn?, 20.ix.??30 (1♂, USNM); **Washington, D.C.** (2♀, BBSL); Rock Creek Park, 28.viii.1919, J.C. Crawford (1♂, AMNH).

**10. *Epeolus barberiellus* Cockerell, 1907**

Figs 2E, 22, 23, & 96E

*Epeolus barberiellus* Cockerell, 1907b. Entomologist 40: 266 (♀).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. barberiellus* apart from all other North American *Epeolus* except *E. americanus* and *E. asperatus*: in females, F2 is not more than 1.1 × as long as wide; the mesoscutum has distinct paramedian bands; the axilla is small to intermediate in size, not extending beyond the midlength of the mesoscutellum and the free portion is less than 1/4 as long as the entire medial length of the axilla, and like the mesoscutellum black; the mesopleuron is closely (i≤1d) and evenly punctate; T1 has a quadrangular discal patch, in dorsal view the longitudinal band is at least as wide as the breadth of the apical fascia; and the T1 and T2 apical fasciae are interrupted or at least greatly narrowed medially. In *E. asperatus* the mesopleuron has much denser punctures ventrolaterally (most i<1d) than that of *E. barberiellus* and the T3 and T4 fasciae are never complete but broken or at

least greatly narrowed laterally, as well as medially into separated or narrowly connected oval patches. *Epeolus barberiellus* is most similar to *E. americanus*, but in *E. americanus* the pronotal lobe and legs are brown or black, not reddish orange.

**Redescription.** FEMALE: Length 5.7 mm; head length 1.8 mm; head width 2.3 mm; fore wing length 5.0 mm.

*Integument coloration*. Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, mesopleuron, metapleuron, propodeum, legs, metasomal terga (including pygidial plate), and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth as dark as mandibular apex (difficult to see in holotype because mandible closed; described from non-type specimens). Pedicel and flagellum brown and orange in part, slightly lighter than dark brown scape. Pronotal lobe reddish brown. Tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black. T5 and pygidial plate reddish orange.

*Pubescence*. Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band and moderately dense pale tomentum along margins. Mesopleuron densely hairy, except for almost entirely bare circular patch occupying much of ventrolateral half of mesopleuron. Metanotum with tomentum uninterrupted, uniformly off white. T1 with median quadrangular reddish-brown discal patch enclosed by pale tomentum, except for medial separation at apex, and narrow, such that longitudinal band more than half as wide as width of discal patch in dorsal view. T2 with fascia interrupted medially and without anterolateral extensions of tomentum, although fascia broader laterally with hairs sparser basally. T3 and T4 with fasciae complete and narrowed laterally. T5 with two patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture*. Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Impunctate spot lateral to lateral ocellus absent in holotype, but shiny spot present in non-type specimens. Mesoscutum, mesoscutellum, and axilla coarsely and densely

rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d), the interspaces shining; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure*. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.9 × greatest width. F2 as long as wide (L/W ratio = 1.0). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5–2 MOD at its terminal (difficult to see in holotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin (L) less than half as long as mesoscutellar width (W) (L/W ratio = 0.3) and tip not extending beyond midlength of mesoscutellum; axilla with tip visible, but unattached to mesoscutellum for less than 1/4 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, nearly as long as wide (L/W ratio = 0.8); S4 and S5 with much longer coppery to silvery subapical hairs, which individually are often darker apically; pygidial plate orange and V-shaped but apically rounded, with large deep punctures closely clustered.

**Distribution:** Arizona to west Texas (Fig. 23).

**Ecology.** HOST RECORDS: The host species of *E. barberiellus* is/are presently unknown.

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Aster* (possibly in reference to a plant that is in a different genus now) (Compositae) and *Sphaeralcea*.

**Discussion.** *Epeolus barberiellus* is most similar to *E. americanus,* from which it differs consistently only in integument coloration. Although sequenced representatives of both forms share the same BIN, specimens identified as *E. barberiellus* cluster separately from those identified as *E. americanus* (Suppl. material 2). Whereas *E. americanus* is widely distributed across North America, *E. barberiellus* appears to be restricted to the Southwestern United States (and possibly adjacent Mexico), where it replaces the much darker form that characterizes *E.*

*americanus*. Taken together, these differences are indicative of divergence, and therefore the two forms are herein considered to be heterospecific. Brumley (1965) also considered *E. americanus* and *E. barberiellus* as separate species, but synonymized *E. asperatus* and *E. melectimimus* under *E. americanus*. In the present study, three valid species in the "*americanus* group" (*E. americanus*, *E. asperatus*, and *E. barberiellus*) are recognized, of which only *E. asperatus* has been assigned a separate BIN, suggesting that *E. americanus* and *E. barberiellus* are sister species.

The male of *E. barberiellus* is described here for the first time. Of the *Epeolus* in the "*americanus* group", this appears to be the least commonly collected species.

**Material studied. Type material.** Primary: USA: **New Mexico:** Mesilla Park, 22.iv.????, C.M. Barber (holotype ♀ [USNM, catalog number: 534039]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAB9110. Specimens examined and sequenced.—USA: **New Mexico:** Sagebrush Valley Rd (32.9500° N; 104.8333° W) (Artesia), 01-10.v.2004, M.E. Irwin (1♂, BBSL).

**Non-barcoded material examined.** USA: **Arizona:** 2 mi SW Apache (Cochise County), 19.iv.1961, Gertsch, Rozen, and Schrammel (1♀, AMNH); 31 mi N Wickenburg, 21.iv.1967, P. Torchio and N. Youssef (1♂, LACM); 40 mi S Kingman (Mohave County), 21.iv.1967, P. Torchio and N. Youssef (1♀, BBSL); **New Mexico:** 12 mi N Las Cruces (Doña Ana County), 11.iv.1965, F.D. Parker (1♂, BBSL); **Texas:** 9.4 mi E Cornudas (Hudspeth County), 27.iv.1998, T., S., and L. Griswold (1♀, BBSL).

**11. *Epeolus basili* new species**

Figs 24, 25, 97D, & 98B

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. basili* apart from all other North American *Epeolus* except *E. nebulosus*, *E. novomexicanus*, and *E. pusillus*: the axilla is large, with the tip extending well beyond the midlength of the mesoscutellum but at most to the

band of pale tomentum along its posterior margin, dilated laterally, and usually ferruginous to some degree (rarely all black) whereas the mesoscutellum ranges from entirely black to partially ferruginous; the axilla's free portion is clearly less than 2/5 as long as its entire medial length; the mesopleuron is closely (most i<1d) and evenly punctate, that of the female is obscured by white tomentum only in the upper half (with a large, sparsely hairy circle occupying much of the ventrolateral half) whereas that of the male (excluding the hypoepimeral area) is entirely obscured by white tomentum; the T1–T3 apical fasciae are complete or only very narrowly interrupted medially; the T2 fascia has lobe-like anterolateral extensions of tomentum; and the pseudopygidial area of the female is lunate with the apex at least 2 × and clearly <2.5 × the medial length. *Epeolus basili*, *E. nebulosus*, *E. novomexicanus*, and *E. pusillus* are all extremely similar to one another. Whereas in *E. pusillus* the flagellum, except sometimes F1, and metasomal sterna are consistently brown or black and clearly not the same reddish-orange color as the legs (tibiae to tarsi), in *E. basili* the flagellum, at least ventrally, is the same reddish-orange color as the legs (tibiae to tarsi) as are usually the metasomal sterna. In *E. nebulosus* and *E. novomexicanus* the T2–T4 fasciae are on or very little removed from the apical margin, and in both species as well as in *E. pusillus* the pseudopygidial area of the female is commonly less and no more than 2 × the medial length. By contrast, in *E. basili* the T2 and T3 (for female) or T2–T4 (for male) fasciae are narrowed medially and removed from the apical margin, and the pseudopygidial area of the female is ≥2 × the medial length. *Epeolus basili* is also similar to *E. scutellaris* in that the axilla is large, with the lateral margin arcuate, and that the apical fasciae are complete or only very narrowly interrupted medially. However, in *E. scutellaris* the pseudopygidial area of the female is even wider (the apex ~2.5–3 × the medial length) than in *E. basili*, and the mesopleuron of both the female and male is obscured by white tomentum only in the upper half (with a large, sparsely hairy circle occupying much of the ventrolateral half).

**Description.** FEMALE: Length 7.0 mm; head length 1.8 mm; head width 2.5 mm; fore wing length 4.8 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, legs, and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth slightly lighter than mandibular apex (difficult to see in holotype; described from paratypes). Antenna brown and

orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black. S1–S5 reddish orange.

*Pubescence.* Face with tomentum densest around antennal socket, slightly sparser on clypeus, upper paraocular and frontal areas, and vertexal area. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron densely hairy, except for sparsely hairy circular patch occupying much of ventrolateral half of mesopleuron. Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally. T1–T3 with apical fasciae complete (basal fascia of T1 also), narrowed medially, and removed from apical margin, most noticeably at midline; T2 with fascia with anterolateral extensions of tomentum. T4 with fascia complete. T5 with large, continuous patch of pale tomentum bordering and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex twice as wide as medial length, indicated by silvery setae on flat disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~2/5 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth obtuse. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.9 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum weakly bigibbous. Axilla large, its lateral margin (L) half as long as mesoscutellar width (W) (L/W ratio = 0.5) and tip extending well beyond midlength of mesoscutellum but not as far back as its posterior margin; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.2); mesopleuron (excluding hypoepimeral area) entirely obscured by white tomentum; S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep, well-separated punctures, with the interspaces shining.

**Etymology.** This species is named in honor of my brother, Basil V. Onuferko (1986–2013).

**Distribution:** Northwestern Mexico and southwestern United States (Fig. 25).

**Ecology.** HOST RECORDS: This species has been collected east of Willcox, Arizona, USA in the presence of large numbers of *Colletes tectiventris* Timberlake (E. Wyman, personal communication, 2014).

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Isocoma hartwegii* (A. Gray) Greene (Compositae), *I. tenuisecta* Greene, *Pectis papposa* Harv. & A. Gray (Compositae), *Psorothamnus scoparius* (A. Gray) Rydb. (Leguminosae), and *Wislizenia refracta* Engelm. (Cleomaceae).

**Discussion.** Structurally, this species is indistinguishable from the other three members of the "*pusillus* group", and although consistent, the features (differences in integument coloration and patterns of pubescence) that in combination may be used to distinguish *E. basili* from *E. nebulosus*, *E. novomexicanus*, and *E. pusillus* are subtle. Its status as a separate species is supported by a separate BIN and large barcode sequence divergence (>7.3%) from its nearest neighbor, *E. pusillus*. In the United States, *Epeolus basili* appears to be restricted to parts of the American Southwest, east of California.

**Material studied. Type material.** Primary: USA: **Arizona:** 4 mi E Willcox (Cochise County), 29.viii.2013, J.S. Ascher (holotype ♀ [CCDB-22791 A05], AMNH).

Secondary: Mexico: **Chihuahua:** 9 mi S Hidalgo del Parral, 31.vii.1967, R.C. Gardner, C.R. Kovacic, and K. Lorenzen (paratype ♂, UCBME); **Durango:** Nombre de Dios,

01.viii.1951, P.D. Hurd (paratypes 1♀, 1♂, EMEC); Otinapa, 11.viii.1947, D. Rockefeller Exp. Michener (paratype ♀, AMNH); Tepehuanes, 1933, Wickham (paratype ♀, USNM).

USA: **Arizona:** 11 mi S San Simon, 02.ix.2013, G. Rowe (paratype ♀, PCYU); 1-3 mi SE Willcox (Cochise County), 25.viii.1994, J.G. Rozen and J.S. Ascher (paratype ♂, AMNH); 2 mi SE Willcox (Cochise County), 05.ix.1986, J.G. and B.L. Rozen (paratype ♀, AMNH); 4 mi E Willcox (Cochise County), 02.ix.2013, C. Lin (paratype ♂, AMNH), 02.ix.2013, Z. Soh (paratypes 2♂, AMNH), 03.ix.2015, R. González Vaquero (paratype ♂, PCYU), 06.ix.2012, J.G Rozen (paratypes 2♀, AMNH), 09.ix.1991, J.G. and B.L. Rozen (paratype ♀, AMNH), 11.ix.1991, J.G. and B.L. Rozen (paratypes 1♀, 2♂, AMNH), 16.ix.2012, E.S. Wyman (paratypes 2♂, AMNH), 16.ix.2012, J.G. and M.A. Rozen (paratype ♀, AMNH), 26.viii.1994, J.G. Rozen and J.S. Ascher (paratypes 3♂, AMNH), 27.viii.2013, E.S. Wyman (allotype ♂ [CCDB-22791 A11], AMNH), 27.viii.2013, E.S. Wyman (paratypes 8♂, AMNH), 27.viii.2013, W.J. Cromartie (paratype ♂, AMNH), 27.viii.2013, G. Rowe (paratypes 7♂ (1 barcoded [CCDB-24580 G03]), PCYU), 28.viii.1985, J.G. and B.L. Rozen (paratypes 8♂, AMNH), 29.viii.2013, J.S. Ascher (paratypes 3♂, AMNH), 30.viii.1993, J.G. Rozen (paratypes 1♀, 9♂, AMNH); E Moore Ranch Rd (32.2391° N; 109.7722° W) (Willcox), 29.viii.2017, R. Oram (paratype ♀, RSKM); Phoenix (Maricopa County), 13.x.1997, K.C. Rozen (paratypes 3♂, AMNH); San Simon (Cochise County), 01.ix.1976, R.M. Bohart (paratype ♂, UCBME); SE Willcox (Cochise County), 30.ix.2016, L. Packer (paratype ♀, PCYU); Willcox (Cochise County), 02.ix.2003, J.G. Rozen, J.S. Ascher, R.L. Staff, and R.E. Edwards (paratypes 2♂, AMNH), 22.ix.1984, J.G. Rozen (paratype ♀, AMNH), 26.ix.1980, J.G. Rozen (paratypes 6♀, AMNH), 28.viii.1958, P.D. Hurd (paratype ♂, UCBME), 28-29.viii.1988, K.V. Krombein and B. Norden (paratype ♂, USNM); **New Mexico:** 5 mi E Laguna (Valencia County), 07.viii.1966, C.R. Kovacic (paratype ♀, UCBME); 20 mi N Animas (Hidalgo County), 05.ix.1981, R.M. Bohart (paratype ♀, UCBME); Mesilla Park, 17.ix.????, T.D. Cockerell (paratype ♀, USNM).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACR5356. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**12. *Epeolus bifasciatus* Cresson, 1864**

Figs 26, 27, & 91A

*Epeolus bifasciatus* Cresson, 1864a. Proc. Entomol. Soc. Phil. 3: 38 (♂); Cresson, 1916. Mem. Am. Entomol. Soc. 1: 113 (♂) [lectotype designation].

**Diagnosis.** Unique to *E. bifasciatus* among North American species of *Epeolus* are each of the following morphological features: the frontal area bears a pair of granulose protrusions, each located near the upper mesal margin of the compound eye; the pronotal collar is elongate, dilated laterally to about 2 × the medial length in dorsal view; and the dorsum of the metasoma has at most two bright orange-yellow fasciae (usually a basal fascia on T1 and always an apical fascia on T2). Similar species occur in Mexico and Central America, but their occurrence in Canada and the United States has not been confirmed.

**Redescription.** This species was recently redescribed (Onuferko 2017).

**Distribution:** United States, east of the Continental Divide, into central Canada (Fig. 27).

**Ecology.** See Onuferko (2017) for host and floral records. Floral associations are also indicated in Suppl. material 1, which includes newly discovered associations with *Coreopsis tinctoria* Nutt. (Compositae) and *Verbena hastata* L. (Verbenaceae) based on labels of examined voucher specimens.

**Discussion.** *Epeolus bifasciatus* is the only species within the "Trophocleptria group" verified as occurring north of Mexico. Originally a genus, *Trophocleptria* Holmberg was later considered a subgenus of *Epeolus* (Michener 2000). Although its constituent species seem to form a natural group, a phylogenetic study by Rightmyer (2004) found that maintaining the subgeneric designation rendered *Epeolus* (*Epeolus*) paraphyletic, so Michener (2007) treated *Trophocleptria* as a distinct species group within *Epeolus*.

*Epeolus fumipennis* Say has been listed as occurring in Kansas (Snow 1879, in which E.T. Cresson was acknowledged for aiding in identification), but was probably confused with *E. bifasciatus*, a species that is common in that state (Ascher and Pickering 2017). Brumley (1965)

examined specimens at the ANSP and KUNHM from the Midwestern and Southeastern United States labelled as *E. fumipennis* that according to him were clearly *E. bifasciatus*. The primary type of *E. fumipennis* was probably destroyed along with much of Thomas Say's insect collection (LeConte 1859:v–vi, xix [footnote]), but the medially-narrowed ferruginous pronotal collar and yellow fasciae on T1 and T2 (contrasting with the whitish fasciae on the remaining terga), as well as its occurrence in Mexico, strongly suggest that this species is in the "Trophocleptria group". However, in *E. fumipennis* the mesoscutum has distinct paramedian bands, which are absent in *E. bifasciatus*, and no specimens from Canada or the United States fitting such a description were seen.

**Material studied. Type material.** Primary: USA: **Illinois:** (lectotype ♂ [ANSP, catalog number: 2658]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ADD5310.
Specimens examined and sequenced.—Canada: **Ontario:** 1♀, 1♂ (PCYU).

USA: **Florida:** 1♂ (FSCA).

**Non-barcoded material examined.** Canada: **Ontario:** 5♀, 6♂ (CNC, DEBU, PCYU, ROM); 2 km N Shiloh (43.7400° N; 80.2675° W) (Wellington County), 08.viii.2004, M. Buck (4♀, DEBU); 6 km NW Saint Williams (42.7050° N; 80.4606° W) (Hard.Norfolk Reg., Manestar Tract), 14.vii.2006, S.M. Paiero (5♀, 1♂, DEBU); Rondeau Park (South Point Trail, Kent County), 29.vi.2002, M. Buck (4♀, 1♂, DEBU); Toronto, 04.viii.2005, A. Cosens (1♂, PCYU).

USA: **Colorado:** Hasty (Bent County), 03.vii.1975, H.E. Evans (1♂, CUM); Longmont (40.1627° N; 105.1441° W) (Boulder County), 17.viii.2012, V. Scott (1♂, CUM); **Florida:** 2♂ (AMNH, PCYU); Caverns State Park (Jackson County), 16.vi.1999, C. Porter and L. Stange (1♀, FSCA); Lake City (Columbia County), 23.vi.2011, S. Lenberger (1♂, FSCA); Lovers Key State Rec Area (Lee County), 12.v.2008, C. Porter and L. Stange (1♀, FSCA); San Felasco Hammock Preserve State Park (Alachua County), 09-12.v.1979, G.B. Fairchild (1♀, FSCA); St Augustine Beach (St. Johns County), 24.v.1992, F.J. Santana (1♂, FSCA); **Georgia:** Athens (Whitehall Preserve, Clarke County), 14-19.v.1979, R.H. Turnbow, Jr. (1♂, FSCA); **Illinois:** 2♀ (AMNH); **Iowa:** Ames, 18.viii.1934, H.A. Scullen (1♀, CUM); **Kansas:** Baldwin, vii.????, J.C.

Bridwell (1♀, CUM); **Maryland:** 2♀ (AMNH, BIML); **Michigan:** 5 km N West Olive (42.9884° N; 86.1423° W) (Ottawa County), 24.viii.2014, J. Gibbs (1♀, JBWM); East Lansing (42.7540° N; 84.4860° W) (Ingham County), 25.viii.2013, J. Gibbs (1♂, JBWM); Near Saline, 26.vi.1954, U.N. Lanham (1♂, CUM); **Missouri:** Rolla (Phelps County), 26.viii.1962, B. Vogel (2♀, CUM); **New York:** 1♂ (BIML); **North Carolina:** 1♂ (AMNH); **Ohio:** West Jefferson, G. Salt (2♀, NHMUK); **Pennsylvania:** 1♂ (BIML); **South Carolina:** 1♂ (DEBU); **South Dakota:** Oacoma (1 km W Chamberlain, Lyman County), 08.viii.2005, R.E. Wrigley (1♀, JBWM); **Texas:** Bentsen-Rio Grande Valley State Park, 01-13.vi.1976, C.C. Porter (1♂, FSCA); McAllen Botanical Gardens (McAllen), 03.vi.1976, C.C. Porter (1♂, FSCA); **Wisconsin:** 1♀ (PCYU).

**13. *Epeolus brumleyi* new species**

Figs 2B, 28, 29, & 103B

*Epeolus brevicornus* Brumley, 1965. M.S. thesis, Utah State University, Logan 38 (♀) [*nomen nudum*].

**Diagnosis.** The following morphological features in combination can be used to tell *E. brumleyi* apart from all other North American *Epeolus*: the frontal carina is weakly convex, such that the supraclypeal area is barely protuberant in lateral view; the mesoscutum has distinct paramedian bands; the axilla is small to intermediate in size, not extending much beyond the midlength of the mesoscutellum (extending to <2/3 its length) but the free portion is at least 1/4 as long as (and less than 2/5) the entire medial length of the axilla, relatively straight along the medial margin, and ferruginous to some degree whereas the mesoscutellum is typically all black; the fore wing has three submarginal cells; the T1 basal and apical fasciae are subparallel; T2–T4 have complete fasciae; and the T2 fascia has a pair of anterolateral extensions of tomentum that are weakly convergent basally. *Epeolus brumleyi* most closely resembles *E. australis*, but in *E. australis* the frontal carina is strongly convex and the pygidial plate of the male is narrower (the medial length is ~1.5 × the basal width) than in *E. brumleyi* (the medial length ≈ the basal width).

**Description.** FEMALE: Length 7.6 mm; head length 1.9 mm; head width 2.7 mm; fore wing length 5.8 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, legs, metasomal terga (including pygidial plate), and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth slightly lighter than mandibular apex (difficult to see in holotype because mandible closed; described from paratypes). Antenna brown and orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron densely hairy, except for two almost entirely bare patches (one beneath base of fore wing (hypoepimeral area), a larger circular patch occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum rubbed off medially in holotype, but uninterrupted and uniformly off white in paratypes. T1 with discal patch elliptical and very wide, the basal and apical fasciae only narrowly joined laterally. T1 with basal fascia complete and apical fascia interrupted medially, T2–T4 with fasciae complete, T2 with fascia with anterolateral extensions of sparser tomentum. T5 with two large patches of pale tomentum lateral to and contacting pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by much more than 1/4 MOD.

*Surface sculpture.* Punctures dense. Labrum with areas of sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d) to rugose, the interspaces shining; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth blunt and obtuse. Labrum with submedial pair of small denticles, apex edentate. Frontal keel not strongly raised. Scape with greatest length 1.8 ×

greatest width. F2 as long as wide (L/W ratio = 1.0). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal (difficult to see in holotype; described from paratypes). Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin (L) less than half as long as mesoscutellar width (W) (L/W ratio = 0.4) and tip not extending beyond midlength of mesoscutellum; axilla with tip visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, nearly as long as wide (L/W ratio = 0.9); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered.

**Etymology.** This species is named after its discoverer, Richard L. Brumley, who recognized it and five other *Epeolus* formally described here (*E. axillaris*, *E. chamaesarachae*, *E. diadematus*, *E. splendidus*, and *E. tessieris*) as new species.

**Distribution:** Arizona to Texas and presumably Mexico, given the close proximity of some collection localities (e.g., Douglas, Arizona) to the Mexico–United States border (Fig. 29).

**Ecology.** HOST RECORDS: I have collected four representatives of this species, at a single site in Southeast Arizona in the spring of 2016 (see Material studied), from or flying near patches of *Chamaesaracha* (A. Gray) Benth. (Solanaceae), which were visited by large numbers of *Colletes* (presumably the host species). Using Stephen's (1954) key, collected females were identified as *C. scopiventer* Swenk (a species known only from females) whereas males were identified (based in part on examination of the terminalia, which were excised) as *C. wickhami* Timberlake (a species known only from males), and sequenced specimens of both sexes were assigned the same BIN (BOLD:AAJ7578).

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Chamaesaracha coniodes* (Moric. ex Dunal) Britton and *Physalis* L. (Solanaceae).

**Discussion.** *Epeolus brumleyi* is a southwestern species that exhibits very little intraspecific morphological variation. Adults have been collected in every month from March to September, and barcoded specimens collected in early May, June, and late August were assigned the same BIN.

**Material studied. Type material.** Primary: USA: **Texas:** Davis Mountains, 10.vii.1942, E.C. Van Dyke (holotype ♀, CAS).

Secondary: USA: **Arizona:** 1 mi E Douglas (Cochise County), 08.v.1989, J.G. Rozen (paratype ♀ [CCDB-28315 G10], AMNH); 14 mi SW Apache (Cochise County), 14.v.1988, J.G. Rozen (paratype ♀, AMNH); 3 mi NE Portal (Cochise County), 18.viii.1970, J.G. Rozen (paratype ♂, AMNH); 3-7 mi S San Simon (Cochise County), 21.v.1988, J.G. Rozen (paratype ♀, AMNH); 9 mi E Douglas (Cochise County), 17.ix.1976, J.G. Rozen (paratype ♂, AMNH); Hwy 80 (31.4450° N; 109.4722° W) (~8 mi NE Douglas, Cochise County), 10.v.2016, T.M. Onuferko (allotype ♂, PCYU), 10.v.2016, T.M. Onuferko (paratypes 2♀ (1 barcoded [CCDB-24580 B11]), 1♂, PCYU); S Blue Sky Road (4 mi E Willcox, Cochise County), 30.viii.2015, J.S. Francis (paratype ♂ [CCDB-28238 A04], PCYU); **New Mexico:** 0.7 km E Longview Spring (32.1007° N; 104.6137° W) (Eddy County), 22.vi.2010, A. Druk and J.D. Herndon (paratype ♀, BBSL); 1 mi W Animas (Hidalgo County), 30.viii.1977, R.W. Brooks (paratype ♀, KUNHM); 1.1 km SW by W Oak Spring (32.1743° N; 104.4580° W) (Eddy County), 11.viii.2010, J.D. Herndon (paratype ♀, BBSL); 4 mi S Animas (Hidalgo County), 24.viii.1974, Rozen and Favreau (paratype ♂, AMNH); Loving (Eddy County), 28.v.1945, J.W. MacSwain (paratype ♂, BBSL); Walnut Canyon (32.1872° N; 104.3936° W) (2.6 km SE by S Cottonwood Spring, Eddy County), 03.vi.2010, A. Druk and J.D. Herndon (paratype ♀, BBSL); **Texas:** 18 km N Coleman (Coleman County), 01.vi.1989, B.N. Danforth (paratype ♀ [CCDB-28315 C09], KUNHM); 2 mi S Falfurrias (Brooks County), 13.iii.1999, J.L. Neff, A. Hook, and C. R. Riley (paratype ♂, CTMI); Davis Mountains, 28.vi.1942, E.C. Van Dyke (paratype ♂, BBSL), 17.iv.1954, R.H. Beamer (paratype ♂, BBSL); Sarita (Kenedy County), 15.iv.1976, J.E. Gillaspy (paratype ♀, BBSL).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACZ9234. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**14. *Epeolus canadensis* Mitchell, 1962**

Figs 30, 31, & 102B

*Epeolus canadensis* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 444 (♀).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. canadensis* apart from all other North American *Epeolus* except *E. compactus* and *E. ferrarii*: in females, F2 is at least 1.2 × as long as wide; the mesoscutum has a small anteromedial patch of pale tomentum; the axilla is small to intermediate in size, not extending much beyond the midlength of the mesoscutellum (extending to <2/3 its length) but the free portion is more than 1/4 as long as the entire medial length of the axilla, and the axilla (except sometimes the tip) and mesoscutellum are black; the mesopleuron is closely (most i<1d) and evenly punctate; and the T2 fascia lacks lobe-like anterolateral extensions of tomentum, although it may be broader laterally. *Epeolus canadensis* differs from *E. compactus* and *E. ferrarii* in the shape of the T1 discal patch, which in *E. canadensis* is distinctly triangular or semicircular (the basal fascia is conspicuously arched and fully continuous with the longitudinal band) and its medial longitudinal extent is more than 1/3 the lateral extent. In *E. compactus* and *E. ferrarii* the shape of the T1 discal patch is variable but typically quadrangular with the basal and apical fasciae subparallel and separated by a distinct longitudinal band. In *E. compactus*, the medially-interrupted T1 basal and apical fasciae may be so broad laterally that they are joined, resulting in a diamond shape with concave sides. In *E. ferrarii* the discal patch may be trapezoidal or almost semicircular, but if at all semicircular its medial longitudinal extent is at most 1/3 the lateral extent and the basal fascia and longitudinal band are at least joined at somewhat of an angle.

**Redescription.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Atlantic Canada to southwestern United States (Fig. 31).

**Ecology.** HOST RECORDS: An association between *Colletes kincaidii* Cockerell and *E. canadensis* hypothesized earlier (Onuferko 2017) seems more likely now based on new knowledge that the two species have been collected in co-occurrence near Six Mile Creek (Ithaca), New York, USA (J. Ascher, personal communication, 2017) and personal collections of the two species in early July, 2017 on the side of a road in Navan (east of Ottawa), Ontario, Canada. *Colletes kincaidii* females and males were collected from staghorn sumac (*Rhus typhina* L. (Anacardiaceae)) on the same dates *E. canadensis* were collected from daisy-like flowers (Compositae) closer to the ground.

FLORAL RECORDS: See Onuferko (2017) for floral records. Floral associations are also indicated in Suppl. material 1, which includes a newly discovered association with *Grindelia* Willd. (Compositae) based on the label of one examined voucher specimen.

**Discussion.** Detailed morphological and taxonomic remarks about this species are given in Onuferko (2017).

**Material studied. Type material.** Primary: Canada: **Nova Scotia:** Ingonish (Cape Breton Island), 07.viii.1928, G. Fairchild (holotype ♀ [MCZ, catalog number: 32859]).

Secondary: USA: **New York:** 9-Mile Creek (Ithaca), 10.vii.1937, P.P. Babiy (allotype ♂ [CUIC, catalog number: 00015611]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ADA0845. Specimens examined and sequenced.—Canada: **Ontario:** 1♀, 1♂ (DEBU); Navan (45.3982° N; 75.3623° W) (Caroltodd Dr & Whispering Willow Dr), 02.vii.2017, T.M. Onuferko (1♂, PCYU), 03.vii.2017, T.M. Onuferko (1♀, PCYU).

USA: **Arizona:** 1♂ (PCYU); Flagstaff (35.1737° N; 111.6756° W) (Coconino County), 01-03.vi.2017, T.M. Onuferko (1♀, PCYU); **New Mexico:** 2♂ (DEBU, PCYU).

**Non-barcoded material examined.** Canada: **Nova Scotia:** 3♀, 4♂ (CNC); **Ontario:** 10♀, 15♂ (CNC, DEBU, PCYU, ROM); Forks of the Credit Provincial Park, vii.2002?, J. Grixti (1♂, PCYU); **Prince Edward Island:** 1♀ (CNC); **Quebec:** 3♀ (CNC).

USA: **Arizona:** 5♀, 3♂ (AMNH, CNC, PCYU); Flagstaff (35.1737° N; 111.6756° W) (Coconino County), 01-03.vi.2017, T.M. Onuferko (1♀, PCYU); Huachuca Mountains, 14.ix.1938, R.H. Crandall (1♀, 1♂, LACM); Santa Catalina Mountains (Pima County), J.L. Neff (1♂, LACM); **Arkansas:** 1♀ (FSCA); **Colorado:** Boulder (Boulder County), 12.ix.1965, U.N. Lanham (1♀, CUM); **Illinois:** 1♀ (KUNHM); **Kansas:** 2♀ (KUNHM); **Missouri:** 1♀ (KUNHM); **New Mexico:** 5♀, 5♂ (AMNH, BBSL, CNC).

**15. *Epeolus carolinus* Mitchell, 1962**

Figs 3C, 32, 33, & 92B

*Epeolus carolinus* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 445 (♂).

**Diagnosis.** The following morphological features in combination can be used to tell *E. carolinus* apart from all other North American *Epeolus*: the mandible has a blunt, obtuse preapical tooth; the axilla is elongate, extending well beyond the midlength of the mesoscutellum but not beyond its posterior margin, and the free portion is distinctly hooked; the mesopleuron is closely (most i<1d) and evenly punctate; and the metasomal fasciae are yellow to orange and interrupted medially. *Epeolus carolinus* resembles *E. deyrupi* in general appearance, but in *E. deyrupi* the axilla is larger, extending as far back as or beyond the posterior margin of the mesoscutellum, and dilated laterally but relatively straight along the medial margin, and the mesopleuron commonly has sparser punctures ventrolaterally (i≤2d) than that of *E. carolinus*, with the interspaces shining or somewhat dull due to tessellate surface microsculpture.

**Redescription.** MALE: Length 6.5 mm; head length 1.8 mm; head width 2.4 mm; fore wing length 5.7 mm.

*Integument coloration*. Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, legs, and pygidial plate. Mandible with apex darker than rest of mandible; preapical tooth

slightly lighter than mandibular apex (difficult to see in holotype; described from paratype). Antenna brown except scape, pedicel, and F1 extensively orange. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum with orange spot anterolaterally between pronotal lobe and tegula. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence*. Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white and yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron densely hairy, except for two sparsely hairy circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum sparser medially, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally by few sparsely scattered pale hairs (not joined in paratype and multiple non-type specimens). T1–T5 with apical fasciae interrupted medially, those of T2–T4 somewhat broader laterally, T2 with fascia without anterolateral extensions of tomentum. T6 with fascia complete. S4 and S5 with long coppery to silvery subapical hairs.

*Surface sculpture*. Punctures dense. Labrum with larger punctures than clypeus, but punctures of both equally dense (i<1d). Impunctate spot lateral to lateral ocellus absent. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), much less so laterally (i>2d). Mesopleuron with ventrolateral half densely punctate (i<1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure*. Preapical tooth inconspicuous, blunt and obtuse. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by less than 1 MOD at its terminal (difficult to see in holotype; described from non-type specimens). Mesoscutellum weakly bigibbous. Axilla large, its lateral margin (L) more than half as long as mesoscutellar width (W) (L/W ratio = 0.6) and tip extending well beyond midlength of mesoscutellum but not as far back as its posterior margin; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin

arcuate and carinate. Fore wing with three submarginal cells. Pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

FEMALE: Description as for male except for usual secondary sexual characters and as follows: F2 even longer than wide (L/W ratio = 1.7); T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on flat disc of apicomedial region elevated from rest of tergum; S4 and S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD); pygidial plate apically truncate, with small, denser punctures.

**Distribution:** South Atlantic states (Fig. 33).

**Ecology.** HOST RECORDS: The host species of *E. carolinus* is/are presently unknown.

FLORAL RECORDS: Mitchell (1962) indicated a floral association with *Eupatorium* L. (Compositae), and BugGuide (http://www.bugguide.net/) indicates an association with *Solidago fistulosa* Mill. Labels of examined voucher specimens further indicate associations with *Euthamia graminifolia* (L.) Nutt. (Compositae), *Heterotheca subaxillaris* (Lam.) Britton & Rusby (Compositae), and *Spermacoce* L. (Rubiaceae).

**Discussion.** This southeastern species is quite variable in terms of integument coloration and pubescence on the metasomal terga. The mesoscutellum and disc of T1 range from entirely black to entirely ferruginous. The axillae appear to be at least partially ferruginous. Whereas T1 and T2 have prominent yellow fasciae, the fasciae on the remaining terga range from prominent to reduced or even absent. Adults of *Epeolus carolinus* are active in September and October.

**Material studied. Type material.** Primary: USA: **North Carolina:** Kill Devil Hills, 12.ix.1956, T.B. Mitchell (holotype ♂ [USNM, catalog number: 534042]).

Secondary: USA: **North Carolina:** Kill Devil Hills, 13.ix.1956, T.B. Mitchell (paratype ♂, NHMUK); New River, 20-30.ix.1944, G.E. Bohart (paratype ♂, BBSL).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACM5698. Specimens examined and sequenced.—USA: **Florida:** Timucuan Ecological & Historic Preserve

(30.3842° N; 81.4857° W) (Duval County), 15.x.2012, C. Pontifet (1♂, BIML); **South Carolina:** Prince George Estates (E Hwy 17, Georgetown County), 09.x.2006, S. Paiero and S.A. Marshall (1♂, DEBU).

**Non-barcoded material examined.** USA: **Florida:** Archbold Biological Station (Highlands County), 11.x.1978, H.V. Weems, Jr. and S.J. Chance (2♀, LACM), 08.x.1964, P.H. Arnaud, Jr. (1♂, LACM); Cedar Key (Levy County), 27.x.1974, E.E. Grissell (3♀, 1♂, UCBME); Doyle Conner Bldg (Gainesville, Alachua County), 04.x.1995, C. Porter (1♂, FSCA), 12.x.1995, C. Porter (1♂, FSCA), 17.x.1995, C. Porter (2♂, FSCA); Gainesville (Alachua County), 13.x.??48 (1♀, LACM), 25.viii.1976, W.H. Pierce (1♂, UCBME); Mason Road (Melrose, Putnam County), 11.x.2009, J.S. Ascher and H.G. Hall (1♂, AMNH); Perry (Taylor County), 1983, L. Packer (1♀, PCYU); W Murdock (Charlotte County), 20.x.1983, L. Packer (2♀, 2♂, PCYU); **South Carolina:** Aiken Savannah River Site (33.3449° N; 81.6614° W), 17.x.2016, S. Breland (1♀, JBWM); Prince George Estates (E Hwy 17, Georgetown County), 09.x.2006, S. Paiero and S.A. Marshall (1♂, DEBU).

**16. *Epeolus chamaesarachae* new species**

Figs 1, 34, 35, 91C, & 92I

*Epeolus lobus* Brumley, 1965. M.S. thesis, Utah State University, Logan 51 (♀) [*nomen nudum*].

**Diagnosis.** *Epeolus chamaesarachae* does not closely resemble any other species of *Epeolus* except *E. diadematus*. Unique in the genus to both species are each of the following morphological features: the vertexal area has two pairs of shiny (usually impunctate) protrusions, the mesoscutum is distinctly ornamented with mostly separate patches of (but some intermixed) pale and ferruginous tomentum, and the T2 fascia has two pairs of anterolateral extensions of tomentum. The difference is that in *E. chamaesarachae* the mesopleuron has sparser punctures ventrolaterally (most i>1d) whereas in *E. diadematus* the mesopleuron has denser (most i≤1d) and more numerous punctures ventrolaterally.

**Description.** FEMALE: Length 7.0 mm; head length 2.0 mm; head width 2.6 mm; fore wing length 5.7 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal collar, pronotal lobe, tegula, axilla, mesoscutellum, and legs. Mandible with apex darker than all but extreme base; preapical tooth lighter than mandibular apex (difficult to see in holotype; described from paratypes). Antenna dark brown except scape, pedicel, and F1 brownish orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Vertexal area with tomentum mostly ferruginous. Dorsum of mesosoma with bands of off-white and ferruginous short appressed setae. Dorsum of metasoma with bands of off-white to pale yellow short appressed setae. Pronotal lobe entirely obscured by pale tomentum. Pronotal collar with tomentum black medially, pale and ferruginous laterally. Mesoscutum with paramedian band of pale tomentum; ferruginous and pale tomentum encircling black spots medially and laterally, respectively, on anterior margin; and ferruginous tomentum along medial mesoscutal line and parapsidal line. Mesopleuron with upper half densely hairy, although scrobe visible; ventrolateral half nearly bare. Metanotum with tomentum uninterrupted, off white laterally and black medially. T1 with median diamond-shaped black discal patch enclosed by pale tomentum, except for medial separation at apex. T1 with apical fascia with black spot posterolaterally. T2–T4 with fasciae interrupted medially, T2 with fascia with paired anterolateral extensions of tomentum. T3 and T4 with fasciae interrupted laterally, with medial portion on apical margin and lateral portion encircling black tomentum on apical margin. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~1/3 MOD.

*Surface sculpture.* Punctures dense, but those of head and mesosoma sparser in some areas, larger, deep, and distinct. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i≤1d). Upper paraocular area and vertexal area with few punctures, the interspaces shining. Mesoscutum, mesoscutellum, and axilla coarsely and densely to sparsely punctate; the

interspaces shining. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with denser (i≤1d) punctures in upper half than ventrolateral half, and ventrolateral half with most interspaces large (i>1d); the interspaces shining. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labral apex with pair of small denticles (preceded by submedial pair of small denticles) separated by shallow concavity and between second pair of apical lobes. Frontal keel strongly raised. Vertexal area with two pairs of impunctate shiny protrusions. Scape with greatest length 1.6 × greatest width. F2 as long as wide (L/W ratio = 1.0). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5 MOD at its terminal. Mesoscutellum strongly bigibbous. Axilla intermediate in size, its lateral margin (L) nearly half as long as mesoscutellar width (W) (L/W ratio = 0.4–0.5) and tip not extending beyond midlength of mesoscutellum; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, but unattached to mesoscutellum for less than 1/3 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, nearly as long as wide (L/W ratio = 0.8); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered apically and sparser basally, with the interspaces shining.

**Etymology.** The name is in reference to the genus of flowers (*Chamaesaracha*) on which the holotype was collected.

**Distribution:** Northwestern Mexico and southwestern United States (Fig. 35).

**Ecology.** HOST RECORDS: The female PCYU paratype collected by H.T. Ngo (see Material studied) is labelled with the same collection information as three *Colletes* specimens (2♀, 1♂) of the presumed host species, which were barcoded and all share the same BIN (BOLD:AAJ7578). Using Stephen's (1954) key, the two females were identified as *C. scopiventer* (a species known only from females) whereas the male was identified (based in part on examination of the terminalia, which were excised) as *C. wickhami* (a species known only from males).

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Baccharis* L. (Compositae), *Chamaesaracha*, *Kallstroemia grandiflora* Torr. ex A. Gray (Zygophyllaceae), *Margaranthus solanaceous* Schltdl. (Solanaceae), *Sphaeralcea angustifolia* (Cav.) G. Don, and *Tidestromia lanuginosa* (Nutt.) Standl. (Amaranthaceae).

**Discussion.** This species and the very similar *E. diadematus* are unusual among *Epeolus* in that the vertexal area has two pairs of shiny (usually impunctate) protrusions, and dorsally the mesosoma and metasoma have unique patterns of ferruginous (mesosoma only) and off-white to pale yellow short appressed setae. *Epeolus chamaesarachae* occurs in the Southwestern United States, and its flight season, based on material examined, is late summer.

**Material studied. Type material.** Primary: USA: **Arizona:** Douglas Model Plane Airport (31.3433° N; 109.4980° W) (Cochise County), 24.viii.2010, T.L. Griswold (holotype ♀ [CCDB-28239 F07], BBSL).

Secondary: Mexico: **Durango:** Durango, 14.viii.1947, D. Rockefeller Exp. Michener (paratype ♂, AMNH); San Juan del Río, 30.vii.1947, D. Rockefeller Exp. Michener (paratype ♀, AMNH).

USA: **Arizona:** 1 mi E Douglas (Cochise County), 16.viii.1962, M. Statham (paratype ♂, AMNH), 27.viii.2007, H.T. Ngo (paratype ♀ [CCDB-22013 G05], PCYU); 1 mi E Douglas (31.3356° N; 109.4950° W) (Cochise County), 23.viii.2003, J.G. Rozen (paratype ♀, AMNH); 12 mi NW Douglas (Cochise County), 30.viii.1989, J.G. and B.L. Rozen and R. Foster (paratype ♀, AMNH); 14 mi SW Apache (Cochise County), 04.viii.1961, J.G. Rozen (paratype ♀, AMNH), 21.viii.2008, J.S. Ascher, J.G. Rozen, and M.A. Rozen (paratype ♂ [CCDB-22791 A09], AMNH); 25 mi SE Sanders (Apache County), 14.viii.1972, J.G. Rozen and R. McGinley (paratype ♂, AMNH); 8 mi NE Portal (Cochise County), 14.viii.1990, J.G. Rozen and J. Krieger (paratype ♀, AMNH); Douglas Model Plane Airport (31.3433° N; 109.4980° W) (Cochise County), 24.viii.2010, T.L. Griswold (allotype ♂ [CCDB-28239 F09], BBSL), 24.viii.2010, T.L. Griswold (paratype ♂, BBSL); Geronimo Trail at Sycamore Creek (31.4432° N; 109.1390° W) (Cochise County), 28.viii.2016, L. Packer (paratype ♀, PCYU); Tombstone (Cochise County), 17.viii.1975, J.G. Rozen (paratype ♀, AMNH); **New Mexico:** 16 mi S Animas (31.7211° N; 108.8224° W) (Hidalgo County), 03.ix.2011, J.G. Rozen and E.S. Wyman (paratype ♀ [CCDB-

22791 A07], AMNH); 2.6 mi E Animas (31.9542° N; 108.7630° W) (NM Hwy 9, 2.6 mi E NM Hwy 338), 11.viii.1972, T.J. Zavortink (paratypes 1♀, 2♂, UCBME); 5.5 mi E Animas (31.9558° N; 108.7142° W) (Hidalgo County), 18-25.viii.2002, E. Elle (paratype ♂, AMNH).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACP9403. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**17. *Epeolus compactus* Cresson, 1878**

Figs 3F, 36, 37, & 38

*Epeolus compactus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 89 (♀, ♂); Cresson, 1916. Mem. Am. Entomol. Soc. 1: 115 (♀) [lectotype designation].
*Epeolus crucis* Cockerell, 1904. Ann. Mag. Nat. Hist. 13: 39 (♀), **syn. n.**
*Epeolus hitei* Cockerell, 1908. Entomologist 41: 60 (♀).
*Triepeolus gabrielis* Cockerell, 1909. Ann. Mag. Nat. Hist. 5: 26 (♂).
*Epeolus geminatus* Cockerell and Sandhouse, 1924. Proc. Calif. Acad. Sci. (4) 13: 315 (♀).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. compactus* apart from all other North American *Epeolus* except *E. canadensis* and *E. ferrarii*: in females, F2 is at least 1.2 × as long as wide; the mesoscutum has a small anteromedial patch of pale tomentum; the axilla is small to intermediate in size, not extending much beyond the midlength of the mesoscutellum (extending to <2/3 its length) but the free portion is more than 1/4 as long as the entire medial length of the axilla, and the axilla (except sometimes the tip) and mesoscutellum are black; the mesopleuron is closely (most i<1d) and evenly punctate; and the T2 fascia lacks lobe-like anterolateral extensions of tomentum, although it may be broader laterally. *Epeolus compactus* is most similar to *E. ferrarii*, and in both species the T1 discal patch is typically quadrangular with the basal and apical fasciae subparallel and separated by a distinct longitudinal band, but in *E. ferrarii* the T2–T4 fasciae are not broadened medially into rounded lobes (as in *E. compactus*) but evenly broad or tapering until separated medially. *Epeolus canadensis* differs from both

species in that the T1 discal patch is distinctly triangular or semicircular (the basal fascia is conspicuously arched and fully continuous with the longitudinal band) and its medial longitudinal extent is more than 1/3 the lateral extent. In *E. compactus*, the medially-interrupted T1 basal and apical fasciae may be so broad laterally that they are joined, resulting in a diamond shape but with concave sides; in *E. canadensis* the lateral sides are straight or convex.

**Redescription.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Western North America (Fig. 37).

**Ecology.** See Onuferko (2017) for host and floral records. Floral associations are also indicated in Suppl. material 1.

**Discussion.** *Epeolus compactus* is a commonly collected species, widespread in Western North America. It is most similar to *E. canadensis* and *E. ferrarii*. In the original description of *E. crucis* Cockerell, the holotype was said to have been initially identified as *E. compactus* by W.J. Fox, but Cockerell (1904) considered it to be distinct, mainly because of differences in coloration and pubescence. The specimen (unusually) has abundant pale tomentum on the discs of the metasomal terga (Fig. 38A), but representatives of several species (e.g., *E. ainsliei*, *E. minimus*, and *E. novomexicanus*) exhibiting atypical abundance of pale tomentum on the mesosoma and metasoma were also observed. Despite the presence of pale tomentum, the discal patch is quadrangular/diamond-shaped (Fig. 38A) as is typical for *E. compactus* (Fig. 38B), and the fascia of T2 is separated medially into rounded lobes. In the *E. crucis* holotype, the axillae and mesoscutellum are (unusually) ferruginous, but it is not unprecedented for species of the genus to have representatives displaying atypical integument coloration. Interestingly, Brumley (1965) treated *E. crucis* as distinct, but the features listed as unique for that species are evident only in the holotype of *E. rufulus*. In fact, his key does not work for the holotypes of *E. crucis* and *E. novomexicanus*, which Brumley believed to be the same species. Unlike in *E. rufulus*, in the *E. crucis* holotype the axillae do not extend beyond the midlength of the mesoscutellum, and the axilla is not conspicuously diverging from the side of the mesoscutellum – the free portion is less than 1/3 as long as the entire medial length of the axilla. As a result of Brumley's work,

specimens of what are actually *E. rufulus* housed at various entomological institutions have been identified (or rather misidentified) as *E. crucis*.

**Material studied. Type material.** Primary: USA: **California:** Mill Creek Canyon (San Bernardino County), 12.ix.1923, E.P. Van Duzee (*E. geminatus* holotype ♀ [CAS, catalog number: 01610]); San Gabriel Mountains (near Pasadena), 15.vii.1909, F. Grinnell, Jr. (*T. gabrielis* holotype ♂ [USNM, catalog number: 534044]); **Colorado:** Copeland Park (Boulder County), 06.ix.1907, G.M. Hite (*E. hitei* holotype ♀ [USNM, catalog number: 534045]); **New Mexico:** Las Cruces, C.H. Townsend (*E. crucis* holotype ♀ [USNM, catalog number: 534043]); **Texas:** G.W. Belfrage (*E. compactus* lectotype ♀ [ANSP, catalog number: 2227]).

Secondary: USA: **Colorado:** (*E. compactus* paralectotype ♀, AMNH).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACU6228. Specimens examined and sequenced.—Canada: **Manitoba:** Birds Hill Provincial Park (50.0114° N; 96.9028° W) (Division 12), 15.vii.2017, J. Gibbs (1♂, JBWM).

USA: **California:** 1♀ (PCYU); **Oregon:** 3♂ (PCYU); **Washington:** 1♀ (PCYU).

**Non-barcoded material examined.** Canada: **Alberta:** 1♀ (KUNHM); **British Columbia:** 2♀, 1♂ (CNC); McIntyre Road (Oliver), 29.v.1958, H. and A. Howden (1♂, CNC); **Saskatchewan:** 1♂ (CNC).

Mexico: **Baja California:** 1 mi W San Borja, 12-13.vi.1967, E.L. Sleeper and E.M. Fisher (1♀, LACM); **Baja California Sur:** 6 km E Insurgentes, 24.iv.1975, E.M. Fisher (1♀, LACM); La Paz and vicinity, 11-14.vi.1975, H. Evans, W. Rubink, and D. Gwynne (1♀, CUM); **Durango:** Durango, 13.viii.1962, A.E. Michelbacher (1♀, EMEC); **Sonora:** 16 mi NW Puerto Peñasco, 29.iii.1965, C.J. McCoy (1♂, CUM).

USA: **Arizona:** 2♀, 1♂ (AMNH, PCYU); 15 mi S Bullhead City (Mohave County), 07.iv.1977, L. Bezark (1♀, UCBME); Oak Creek Valley Road (Yavapai County), 16.vi.1978, R.C. Miller (1♀, UCBME); **California:** 1♀, 3♂ (AMNH, FSCA); Andreas Canyon (Riverside County), 30.iii.1977, R.M. Bohart (1♂, UCBME); Arroyo Seco Campground (Monterey County), 19.v.1964, F.D. Parker (1♀, UCBME); 19.v.1964, R.M. Bohart (1♂, UCBME), 23.vii.1967, R.F. Denno (1♀, UCBME); Charlton Flats (San Gabriel Mountains), 08.ix.1977,

A.S. Menke (1♀, UCBME); Felton Springs (Santa Cruz County), 16.vi.1973, R.M. Bohart (1♂, UCBME); Granite Mountains (San Bernardino County), 10.x.1977, N.J. Smith (1♀, UCBME), 10.x.1977, R.M. Bohart (1♀, UCBME); Mojave (Kern County), 23.v.1978, R.P. Meyer (2♂, UCBME); Peña Spring (San Diego County) (1♀, BBSL); Thousand Palms (Riverside County), 11.iv.1970, E.E. Grissell (1♀, UCBME); **Colorado:** 3♀ (AMNH, PCYU); **Nevada:** Kings Canyon (5 mi W Carson City), 07.viii.1975, B. Villegas (1♂, UCBME); **New Mexico:** 8♂ (AMNH, PCYU); Granite Gap (18 mi N Rodeo, Hidalgo County), 07.ix.1976, R.M. Bohart (1♀, UCBME); **Oklahoma:** 1♀ (FSCA); **Oregon:** 1♂ (PCYU); **Texas:** 7.6 mi S Van Horn (Culberson County), 27.iv.1979, R.R. Snelling (1♀, LACM); Rd 1108 (4-8 mi SE 652, Culberson County), 14.vi.2005, J.L. Neff and A. Hook (1♂, CTMI); Z H Canyon (30.0920° N; 104.6620° W) (Presidio County), 19.v.2005, J.L. Neff and A. Hook (1♀, CTMI); **Washington:** 1♀ (PCYU); **Wyoming:** 1♀, 2♂ (AMNH).

**18. *Epeolus deyrupi* new species**

Figs 39, 40, & 92C

**Diagnosis.** The following morphological features in combination can be used to tell *E. deyrupi* apart from all other North American *Epeolus*: the axilla is large, with the tip extending well beyond the midlength of the mesoscutellum, dilated laterally, and like the mesoscutellum ferruginous; the mesopleuron commonly has sparser punctures ventrolaterally (i≤2d) than in upper half, with the interspaces shining or somewhat dull due to tessellate surface microsculpture; and the T1–T3 apical fasciae are interrupted and (to varying degrees) brownish orange medially and off white laterally. *Epeolus deyrupi* resembles *E. andriyi*, *E. floridensis*, *E. howardi*, and *E. packeri* in that the axilla is large, with the lateral margin arcuate, and like the mesoscutellum ferruginous, and that the T1–T3 apical fasciae are interrupted medially. However, in *E. deyrupi* the pseudopygidial area of the female is wider (the apex >2 × the medial length) than in *E. andriyi*, *E. floridensis*, or *E. howardi* (the apex <2 × the medial length), and the T1 basal fascia is absent or reduced to a pair of small patches of pale tomentum whereas in *E. andriyi*, *E. floridensis*, and *E. howardi* T1 has a distinct, although often medially-interrupted, basal fascia. *Epeolus deyrupi* closely resembles *E. packeri*, but in *E. packeri* the mesopleuron has

denser punctures ventrolaterally (most i<1d) than that of *E. deyrupi* and the metasomal terga have pale but not brownish orange pubescence.

**Description.** FEMALE: Length 8.8 mm; head length 2.2 mm; head width 2.9 mm; fore wing length 6.1 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, labrum, clypeus, antenna, pronotal collar, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, metanotum, mesopleuron, metapleuron, propodeum, and legs. Mandible with apex darker than rest of mandible; preapical tooth lighter than mandibular apex (difficult to see in holotype because mandible closed; described from paratypes). Antenna brown and orange in part. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum reddish brown laterally and posteriorly. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white and brownish orange short appressed setae. Mesoscutum with paramedian band. Mesopleuron mostly bare, but tomentum moderately dense ventrally as well as between two almost entirely bare patches (one beneath base of fore wing (hypoepimeral area), a larger circular patch occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted except for median bare patch in posterior half (also bare along posterior margin), uniformly off white. T1 with basal fascia reduced to pair of small patches of off-white tomentum; T1–T4 with apical fasciae brownish orange medially and off white laterally, and medially interrupted and removed from apical margin; T2 with fascia without anterolateral extensions of tomentum. T4 with fascia interrupted laterally. T5 with two patches of pale tomentum bordering and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with denser (i≤1d) punctures in upper

half than ventrolateral half (i≤2d), the interspaces somewhat dull due to tessellate surface microsculpture. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth obtuse. Labral apex with pair of small denticles, each preceded by longitudinal carina. Frontal keel not strongly raised. Scape with greatest length 1.7 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.2). Preoccipital ridge not joining hypostomal carina, from which it is separated by less than 1 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla large, its lateral margin (L) more than half as long as mesoscutellar width (W) (L/W ratio = 0.6) and tip nearly extending as far back as apex of horizontal dorsal portion of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, not noticeably longer than wide (L/W ratio = 1.1); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate with apex slightly concave and large deep punctures closely clustered basally and sparser apically, with the interspaces shining.

**Etymology.** This species is named after its discoverer, Dr. Mark A. Deyrup, who recognized it as a new species and brought his discovery to my attention.

**Distribution:** Florida and coastal Georgia (Fig. 40).

**Ecology.** HOST RECORDS: The host species of *E. deyrupi* is/are presently unknown.

FLORAL RECORDS: Labels of examined voucher specimens indicate a floral association with *Sideroxylon tenax* L. (Sapotaceae).

**Discussion.** *Epeolus deyrupi* is a southeastern species that exhibits very little intraspecific morphological variation. Most of the known specimens of this species were collected in Highlands County, Florida. Based on known records, adults of *E. deyrupi* are active in spring.

**Material studied. Type material.** Primary: USA: **Florida:** Flamingo Villas Preserve (27.4423° N; 81.3782° W) (Highlands County), 26.v.2009, M. Deyrup, A. May, and H. Otte (holotype ♀ [CCDB-24583 F06], FSCA).

Secondary: USA: **Florida:** Allen David Broussard Catfish Creek Preserve State Park (27.8503° N; 81.4954° W) (Polk County), 08.vi.2009, M. Deyrup, A. May, and H. Otte (paratype ♂, ABS); Archbold Biological Station (27.1239° N; 81.3661° W) (Highlands County), 21.vi.2010, M. and L. Deyrup (paratype ♀, ABS); Archbold Biological Station (Highlands County), 29.v.1979, H.V. Weems, Jr. and S. Halkin (paratype ♀, LACM), 14.vi.2010, M. and L. Deyrup (paratype ♀, ABS); Flamingo Villas Preserve (27.4423° N; 81.3782° W) (Highlands County), 25.v.2009, M. Deyrup, A. May, and H. Otte (paratype ♀, ABS); Flamingo Villas Preserve (27.4487° N; 81.3767° W) (Highlands County), 01.vi.2009, M. Deyrup, A. May, and H. Otte (paratype ♀, ABS); Gould Rd Preserve (27.1336° N; 81.3256° W), 25.v.2009, M. Deyrup, A. May, and H. Otte (paratype ♀, PCYU), 26.v.2009, M. Deyrup, A. May, and H. Otte (paratype ♀, ABS); Lake Placid (Archbold Biological Station, Highlands County), 12.vi.1983, M. Deyrup (paratype ♀, ABS), 11.vi.1986, M. Deyrup (paratype ♀, ABS); The Nature Conservancy Tiger Creek Preserve (27.8077° N; 81.4816° W) (Polk County), 04.vi.2010, J. Dunlap, M. and N. Deyrup, and K. Dearborn (paratype ♀ [CCDB-24583 H04], PCYU); Tiger Creek Preserve (27.8133° N; 81.4868° W) (Polk County), 12.vi.2010, J. Dunlap, M. and N. Deyrup, and K. Dearborn (paratype ♀ [CCDB-24583 H02], USNM); **Georgia:** St Catherines Island (Liberty County), 24-27.vi.1989, Rozen, Quinter, and Eickwort (allotype ♂, AMNH), 27.vi.1974, R.O. Schuster and E.C. Teftner (paratype ♂, UCBME).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ADF0241. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**19. *Epeolus diadematus* new species**

Figs 41, 42, & 92J

*Epeolus torus* Brumley, 1965. M.S. thesis, Utah State University, Logan 71 (♀) [*nomen nudum*].

**Diagnosis.** *Epeolus diadematus* does not closely resemble any other species of *Epeolus* except *E. chamaesarachae*. Unique in the genus to both species are each of the following morphological features: the vertexal area has two pairs of shiny (usually impunctate) protrusions, the mesoscutum is distinctly ornamented with mostly separate patches of (but some intermixed) pale and ferruginous tomentum, and the T2 fascia has two pairs of anterolateral extensions of tomentum. The difference is that in *E. diadematus* the mesopleuron has denser punctures ventrolaterally (most i≤1d) whereas in *E. chamaesarachae* the mesopleuron has sparser (most i>1d) and fewer punctures ventrolaterally.

**Description.** FEMALE: Length 6.9 mm; head length 2.0 mm; head width 2.6 mm; fore wing length 6.0 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal collar, pronotal lobe, tegula, axilla, mesoscutellum, and legs. Mandible with apex darker than all but extreme base; preapical tooth lighter than mandibular apex. Antenna dark brown except scape, pedicel, and F1 brownish orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Vertexal area with tomentum mostly ferruginous. Dorsum of mesosoma with bands of off-white and ferruginous short appressed setae. Dorsum of metasoma with bands of off-white to pale yellow short appressed setae. Pronotal collar with tomentum black medially, pale and ferruginous laterally. Mesoscutum with paramedian band of pale tomentum; ferruginous and pale tomentum encircling black spots medially and laterally, respectively, on anterior margin; and ferruginous tomentum along medial mesoscutal line and parapsidal line. Mesopleuron with upper half densely hairy, although scrobe visible; ventrolateral half nearly bare. Metanotum with tomentum uninterrupted, off white laterally and black medially. T1 with median diamond-shaped black discal patch enclosed by pale tomentum, except for medial separation at apex. T1 with apical fascia with black spot posterolaterally. T2–T4 with fasciae interrupted medially, T2 with fascia with paired anterolateral extensions of tomentum. T3 and T4 with fasciae interrupted laterally, with medial portion on apical margin and lateral portion encircling black tomentum on apical margin. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5

with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~1/3 MOD.

*Surface sculpture.* Punctures dense, but those of head and mesosoma sparser in some areas, larger, deep, and distinct. Labrum mostly with larger and sparser punctures (i=1–2d) than clypeus (i≤1d). Upper paraocular area and vertexal area sparsely punctate (i=1–2d), the interspaces shining. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate; the interspaces shining. Tegula densely punctate mesally (i=1–2d), much less so laterally (i>2d). Mesopleuron with denser (i<1d) punctures in upper half than ventrolateral half, although ventrolateral half with most interspaces small (i≤1d); the interspaces shining. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labral apex with two pairs of small denticles (the middlemost pair preceded by submedial pair of small denticles and separated by shallow concavity). Frontal keel strongly raised. Vertexal area with two pairs of nearly impunctate shiny protrusions. Scape with greatest length 1.6 × greatest width. F2 as long as wide (L/W ratio = 1.0). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum strongly bigibbous. Axilla intermediate in size, its lateral margin (L) nearly half as long as mesoscutellar width (W) (L/W ratio = 0.4–0.5) and tip not extending much beyond midlength of mesoscutellum (extending to <2/3 its length); axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, but unattached to mesoscutellum for less than 1/3 the medial length of axilla; axilla with lateral margin somewhat arcuate. Fore wing with three submarginal cells. Pygidial plate mostly hidden in holotype, but apically truncate in paratypes.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, nearly as long as wide (L/W ratio = 0.8); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered apically and sparser basally, with the interspaces shining.

**Etymology.** The name is in reference to the four shiny, usually impunctate, tubercles on the vertexal area of the head of this species. From the Latin, “diadema” (royal headband).

**Distribution:** Texas and presumably Mexico, given the close proximity of some collection localities (e.g., Southmost, Texas) to the Mexico–United States border (Fig. 42).

**Ecology.** HOST RECORDS: The host species of *E. diadematus* is/are presently unknown.

FLORAL RECORDS: The label of one examined voucher specimen indicates a floral association with *Engelmannia pinnatifida* A.Gray ex Nutt. (Compositae). This species has also been collected from *Aphanostephus riddellii* Torr. & A. Gray (Compositae) (J. Neff, personal communication, 2016).

**Discussion.** This species and *E. chamaesarachae* are very similar in terms of integument coloration, pubescence, and structure, and are presumably sister species. Specimens of *E. diadematus* are distinct from those designated as *E. chamaesarachae* in that the mesopleuron has much denser punctation. The status of *E. diadematus* as a separate species is further supported by a separate BIN and large barcode sequence divergence (3.2%) from its nearest neighbor, *E. chamaesarachae* (Suppl. material 2). The ranges and flight seasons of these species also differ. With one exception, examined specimens of *E. diadematus* were collected in spring, and all are from Coastal or South Texas. By contrast, *E. chamaesarachae* occurs further west in the United States, and adults are active in late summer.

**Material studied. Type material.** Primary: USA: **Texas:** McAllen Botanical Gardens (McAllen), 21.xi.1982, C. Porter (holotype ♀, FSCA).

Secondary: USA: **Texas:** 5 mi SE Realitos (27.3980° N; 98.5490° W) (Duval County), 22.iv.2005, J.L. Neff and A. Hook (paratype ♂, CTMI); Ben Bolt (Jim Wells County), 12.v.1952, M. Cazier, W. Gertsch, and R. Schrammel (paratype ♀, AMNH); Brackenridge Field Laboratory (Austin, Travis County), 28.iv.1989, A. Hook (paratype ♂, CTMI); Chaparral Wildlife Management Area (Dimmit County), 06.iv.2007, J.L. Neff and A. Hook (paratype ♂, CTMI), 11.iv.2003, J.L. Neff and A. Hook (paratype ♂, CTMI); Dallas, 22.v.??06, W.D. Pierce (paratypes 2♂, USNM); Galveston?, L. Packer (paratype ♀ [CCDB-30383 F06], PCYU); Southmost (Cameron County), 13.vi.1953, Univ. Kans. Mex. Expedition (allotype ♂, KUNHM).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ADJ9659. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**20. *Epeolus erigeronis* Mitchell, 1962**

Figs 43, 44, & 92E

*Epeolus erigeronis* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 445 (♀).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. erigeronis* apart from all other North American *Epeolus* except *E. ilicis* and *E. inornatus*: the mandible is simple; the axilla does not attain the midlength of the mesoscutellum but the free portion is distinctly hooked, with the tip unattached to the mesoscutellum for more than 1/3 of the entire medial length of the axilla; the pronotal collar and metasomal terga are black; the metasomal terga have rather fine punctures; and the pseudopygidial area of the female is distinctly campanulate with the apex <2 × the medial length and not in contact with two large patches of pale tomentum (one on each side) throughout its length (in contact only at apex, diverging basally). Although in all three species the mesopleuron is closely and evenly punctate, in *E. erigeronis* the punctures are more variable in size, with many smaller punctures among large ones, and most interspaces are narrower such that the surface appears to be very coarsely and densely rugose-punctate. By contrast, in *E. ilicis* and *E. inornatus* the mesopleuron has punctures that are similar in size and shiny interspaces that are commonly equal to the puncture diameters.

**Redescription.** FEMALE: Length 8.6 mm; head length 2.2 mm; head width 3.0 mm; fore wing length 6.3 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, and legs. Mandible with apex darker than all but extreme base. Antenna brown except scape, pedicel, and F1 orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, except beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum uninterrupted except for median bare patch in posterior half, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally. T1 and T2 with apical fasciae interrupted medially, those of T2 and T3 somewhat broader laterally, T2 with fascia with faint anterolateral extensions of sparser tomentum. T3 and T4 with fasciae complete. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area campanulate, its apex less than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 1/3 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger punctures than clypeus, but punctures of both equally dense (i<1d). Small impunctate matte spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half coarsely and densely rugose-punctate (i<1d), the interspaces somewhat dull due to surface microsculpture; mesopleuron with many smaller punctures among large ones, punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i=1–2d), evenly distributed on disc; the interspaces shining somewhat.

*Structure.* Mandible without preapical tooth. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.6). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum weakly bigibbous. Axilla intermediate in size, its lateral margin (L) nearly half as long as mesoscutellar width (W) (L/W ratio = 0.4–0.5) and tip attaining midlength of mesoscutellum; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin arcuate and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.3); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered basomedially and sparser apically and laterally, with the interspaces shining.

**Distribution:** South Atlantic states (Fig. 44).

**Ecology.** HOST RECORDS: The host species of *E. erigeronis* is/are presently unknown.

FLORAL RECORDS: Mitchell (1962) indicated floral associations with *Erigeron quercifolius* Lam. (Compositae), *Hypericum* L. (Hypericaceae), and *Melilotus albus* Medik. (Leguminosae). Labels of examined voucher specimens further indicate associations with *Clinopodium ashei* (Weath.) Small (Lamiaceae), *Ilex glabra* (L.) A. Gray (Aquifoliaceae), and *Vaccinium darrowii* Camp (Ericaceae).

**Discussion.** *Epeolus erigeronis* exhibits very little intraspecific morphological variation. However, in some specimens the axillae are partially ferruginous whereas in others they and the mesoscutellum are entirely black. Based on examined records, adults of *E. erigeronis* are active throughout spring.

Although BIN-compliant sequences are presently not available for *E. erigeronis*, four partial sequences (three 422 bp and one 394 bp in length) are available for specimens from North and South Florida, and these sequences form a distinct cluster that does not include any sequences from other *Epeolus* species in a NJ tree (Suppl. material 2).

**Material studied. Type material.** Primary: USA: **Florida:** Levy County, 13.iv.1955, H.V. Weems, Jr. (holotype ♀, FSCA).

Secondary: USA: **Florida:** Alachua County, 15.iv.1955, R.A. Morse (paratype ♀, FSCA); Levy County, 13.iv.1955, H.V. Weems, Jr. (allotype ♂, FSCA); **North Carolina:** Southport, 24.vi.1928, T.B. Mitchell (paratype ♀, NHMUK).

**DNA barcoded material with BIN-compliant sequences.** Unavailable.

**Non-barcoded material examined.** USA: **Florida:** 5 mi S Paynes Prairie (SE Gainesville, Alachua County), 05-12.v.1996, B.D. Sutton (1♀, FSCA); Apalachicola National Forest (30.3292° N; 84.5052° W) (Wakulla County), 08-15.v.2005, Ronquist lab (1♀, PCYU); Archbold Biological Station (Highlands County), 10.v.1979, H.V. Weems, Jr. and S. Halkin (1♀, BBSL), 17-23.iv.2007, S.M. Paiero (1♂, DEBU), 17.v.2005, M. Deyrup (1♀, ABS), 08.iv.1980, H.V. Weems, Jr. and F.E. Lohrer (1♀, FSCA), 24.iii.1980, H.V. Weems, Jr. and F.E. Lohrer (1♂, FSCA); Archbold Biological Station (27.1838° N; 81.3532° W) (Highlands County), 23.v.2010, M. Deyrup (1♀, ABS), 28.v.2010, M. Deyrup (1♀, ABS); Austin Cary Forest (Gainesville, Alachua County), 10.vi.1976 (1♂, UCBME), 16.x.1977, G.B. Fairchild (1♀, UCBME), 17.v.1991, L.R. Davis, Jr. (1♀, FSCA), 20.vi.1978, G.B. Fairchild and H.V. Weems, Jr. (1♀, UCBME); Brighton, 07.iv.1937, H.I. Scudder (1♀, CAS); Flamingo Villas Preserve (27.4487° N; 81.3767° W) (Highlands County), 01.vi.2009, M. Deyrup, A. May, and H. Otte (1♀, ABS); Flamingo Villas Preserve (27.4515° N; 81.3854° W) (Highlands County), 05.v.2010, M. Deyrup and J. Dunlap (1♀, ABS); Highlands Hammock State Park, 14.iv.1968, H.V. Weems, Jr. (2♀, FSCA); Kincaid Road (SE Gainesville, Alachua County), 03.iv.1999, B.D. Sutton (1♀, FSCA); Lake Placid (27.2195° N; 81.3803° W) (Highlands County), 14.iv.2010, M. Deyrup and J. Dunlap (1♀, ABS); New Smyrna Beach, 14.iii.1943, R.L. Usinger (1♂, EMEC); Osceola National Forest (Baker County and Columbia County line), 13-26.iv.1977, J.R. Wiley (1♂, FSCA), 01.v.2011, S. Lenberger (1♀, FSCA); San Felasco State Hammock Preserve, 16.v.1977, G.B. Fairchild and H.V. Weems, Jr. (1♀, UCBME).

**21. *Epeolus ferrarii* new species**

Figs 45 & 46

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. ferrarii* apart from all other North American *Epeolus* except *E. canadensis* and *E. compactus*: in females, F2 is at least 1.2 × as long as wide; the mesoscutum has a small anteromedial patch of pale tomentum; the axilla is small to intermediate in size, not extending much beyond the midlength of the mesoscutellum (extending to <2/3 its length) but the free portion is more than 1/4 as long as the entire medial length of the axilla, and the axilla (except sometimes the tip) and mesoscutellum are black; the

mesopleuron is closely (most i<1d) and evenly punctate; and the T2 fascia lacks lobe-like anterolateral extensions of tomentum, although it is broader laterally. *Epeolus ferrarii* is most similar to *E. compactus*, and in both species the T1 discal patch is typically quadrangular with the basal and apical fasciae subparallel and separated by a distinct longitudinal band, but in *E. compactus* the T2–T4 fasciae are not evenly broad or tapering until separated medially (as in *E. ferrarii*) but broadened medially into rounded lobes, which may be joined or separated. *Epeolus canadensis* differs from both species in that the T1 discal patch is distinctly triangular or semicircular (the basal fascia is conspicuously arched and fully continuous with the longitudinal band) and its medial longitudinal extent is more than 1/3 the lateral extent. In *E. ferrarii* the discal patch may be trapezoidal or almost semicircular, but if at all semicircular its medial longitudinal extent is at most 1/3 the lateral extent and the basal fascia and longitudinal band are at least joined at somewhat of an angle.

**Description.** MALE: Length 7.1 mm; head length 1.9 mm; head width 2.6 mm; fore wing length 6.0 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, legs, and pygidial plate. Mandible with apex and preapical tooth darker than all but basal quarter. Antenna brown except F1 extensively orange. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs from tibia to tarsus extensively reddish orange. Pygidial plate orange along apical margin, otherwise dark brown.

*Pubescence.* Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with anteromedial horseshoe-shaped patch of pale tomentum. Mesopleuron densely hairy, except for two sparsely hairy circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted, pale yellow laterally and black medially. T1 with median elliptical verging on semicircular discal patch. T1–T3 with apical fasciae medially interrupted, narrowed (broader laterally), and removed from apical margin; T2 with fascia without anterolateral extensions of

tomentum. T4–T6 with fasciae complete, those of T4 and T5 somewhat narrowed medially. S4 and S5 with long coppery to silvery subapical hairs, which individually are often darker apically.

*Surface sculpture.* Punctures dense. Labrum with larger punctures than clypeus, but punctures of both equally dense (i≤1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half coarsely and densely punctate (i<1d) to rugose; mesopleuron with punctures more or less equally dense throughout (only few i=1d ventrolaterally). Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labral apex with pair of small denticles, each preceded by longitudinal carina. Frontal keel not strongly raised. Scape with greatest length 1.8 × greatest width. F2 as long as wide (L/W ratio = 1.0). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5 MOD at its terminal (difficult to see in holotype; described from paratypes). Mesoscutellum weakly bigibbous. Axilla small to intermediate in size, its lateral margin (L) less than half as long as mesoscutellar width (W) (L/W ratio = 0.4) and tip not extending much beyond midlength of mesoscutellum (extending to <2/3 its length); axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically rounded, with large deep punctures closely clustered medially and sparser laterally, with the interspaces shining.

FEMALE: Description as for male except for usual secondary sexual characters and as follows: F2 slightly but not noticeably longer than wide (L/W ratio = 1.1); T5 with large, nearly continuous patch of pale tomentum bordering and separate from pseudopygidial area present only in female; T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum; S4 and S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~1/3 MOD); pygidial plate apically truncate, with small, denser punctures.

**Etymology.** This species is named in honor of my colleague, Rafael Ferrari, with whom I collected this species in Southwestern New Mexico, USA.

**Distribution:** Arizona and New Mexico to southeastern Mexico (Fig. 46).

**Ecology.** HOST RECORDS: The host species of *E. ferrarii* is/are presently unknown.

FLORAL RECORDS: Labels of examined voucher specimens indicate a floral association with *Melilotus albus*.

**Discussion.** *Epeolus ferrarii* is a cryptic species that most closely resembles *E. canadensis* and *E. compactus*, and can only be differentiated from these two species on the basis of very subtle differences in the patterns of pubescence on the metasomal terga. Its status as a separate species is supported by a separate BIN, but unusually its nearest neighbor is *E. splendidus* (a very different species, although presumably in the same species group), from which *E. ferrarii* exhibits a large barcode sequence divergence (3.9%). Although most species of *Epeolus* were described from a female name-bearing type, a male specimen is designated as the holotype of *E. ferrarii* because a barcode-compliant sequence is associated with it and because the collection locality is more precise than for the available female specimens, one of which is herein designated as the allotype.

**Material studied. Type material.** Primary: USA: **New Mexico:** 47 km S Animas (31.5438° N; 108.8757° W) (Co Rd C001), 30.viii.2015, R. Ferrari and T.M. Onuferko (holotype ♂ [CCDB-24583 H08], PCYU).

Secondary: Guatemala: **Zacapa:** San Lorenzo, xi.1986, M. Sharkey (paratype ♂, CNC).

Mexico: **Chiapas:** Yerbabuena (20 mi N Bochil), 21.v.1969, W.R.M. Mason (paratype ♂, CNC); **Hidalgo:** 2 mi N Pachuca, 24.viii.1962, M.G. Naumann (paratype ♀, KUNHM); **Nuevo León:** Cola de Caballo, 20.vi.1976, D. Weems (paratype ♂, FSCA); **Puebla:** 5 mi NE Teziutlán, 20.vi.1961, Univ. Kans. Mex. Expedition (paratype ♀, KUNHM); **Veracruz:** 10 km N Coscomatepec, 09.vii.1974, J.A. Chemsak, E. and J. Linsley, and J. Powell (paratype ♀, EMEC).

USA: **Arizona:** Southwestern Research Station (5 mi W Portal, Cochise County), 01.viii.1956, C. and M. Cazier (paratype ♀, AMNH), 02.viii.1956, C. and M. Cazier (paratype ♀, AMNH); **New Mexico:** 47 km S Animas (31.5438° N; 108.8757° W) (Co Rd C001),

30.viii.2015, R. Ferrari and T.M. Onuferko (paratypes 2♂ (1 barcoded [CCDB-24580 G07]), PCYU), 30.viii.2015, C. Parsons (paratype ♂, PCYU); 5 mi N Alamogordo (Otero County), 24.iv.1965, O.W. Richards (paratype ♀, NHMUK); Granite Gap (18 mi N Rodeo, Hidalgo County), 07.ix.1976, R.M. Bohart (allotype ♀, UCBME), 07.ix.1976, R.M. Bohart (paratypes 1♀, 1♂, UCBME); **Texas:** 23 mi W Fort Davis, 01.vi.1959, W.R.M. Mason (paratype ♀, CNC); Big Bend National Park, 04.vi.1970, C.W. O'Brien (paratype ♀, LACM); Grapevine Spring (Big Bend National Park), 20.v.1959, W.R.M. Mason (paratype ♀, CNC); Dugout Wells (Big Bend National Park), 22.v.1959, J.F. McAlpine (paratypes 3♀, CNC); Sanderson, 28-29.iv.1959, W.R.M. Mason (paratype ♀, CNC).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ADD6263. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**22. *Epeolus flavofasciatus* Smith, 1879**

Figs 2C, 47, & 48

*Epeolus flavofasciatus* Smith, 1879. Descr. New Species Hymen.: 103 (♀, ♂), **new lectotype designation**

*Triepeolus flavofasciatus* Cockerell 1904. Ann. Mag. Nat. Hist. 13: 36.

*Triepeolus agaricifer* Cockerell, 1907c. Ann. Mag. Nat. Hist. 20: 60 (♂).

**Diagnosis.** The following morphological features in combination can be used to tell *E. flavofasciatus* apart from all other North American *Epeolus*: the dorsum of the mesosoma and metasoma have bright or pale yellow pubescence, the mesoscutum has distinct paramedian bands, the axilla does not attain the midlength of the mesoscutellum, and T1 has a median triangular or semicircular discal patch. *Epeolus canadensis* resembles *E. flavofasciatus* in that the integument is mostly black, the axilla does not attain the midlength of the mesoscutellum, and T1 has a median triangular or semicircular discal patch, but in *E. canadensis* the mesoscutum has a distinct anteromedial patch of pale tomentum instead of paramedian bands. *Epeolus flavofasciatus* is quite large for *Epeolus* (≥9 mm in length), and the pygidial plate of the male is

narrower than that in most species, so males may be confused with *Triepeolus*. However, in *E. flavofasciatus* the mandible has a blunt, obtuse preapical tooth, whereas in all *Triepeolus* the mandible is simple.

**Redescription.** FEMALE: Length 9.6 mm; head length 2.4 mm; head width 3.3 mm; fore wing length 8.5 mm.

*Integument coloration*. Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, legs, and pygidial plate. Mandible with apex darker than all but extreme base; preapical tooth lighter than mandibular apex (difficult to see in the *E. flavofasciatus* lectotype because mandible closed; described from non-type specimens). Antenna brown except scape, pedicel, and F1 extensively orange. F2 with orange spot basally. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane dusky subhyaline, slightly darker at apex. Legs more extensively reddish orange than brown or black.

*Pubescence*. Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white and bright to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron sparsely hairy except mesally with densely hairy sigmoid patch and ventrally. Metanotum with tomentum uninterrupted, uniformly black (uniformly pale yellow in the *E. agaricifer* holotype and multiple non-type specimens, uniformly black or to varying degrees bright or pale yellow laterally and black medially in other non-type specimens). T1 with median semicircular black discal patch enclosed by pale tomentum (basal fascia widely separated medially and with much tomentum rubbed off in the *E. flavofasciatus* lectotype, but conspicuously arched and narrowly interrupted medially in non-type specimens). T2–T4 with fasciae complete, T2 with fascia without anterolateral extensions of tomentum. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by much more than 1/4 MOD.

*Surface sculpture*. Punctures dense. Labrum with larger punctures than clypeus, but punctures of both equally dense (i<1d). Small impunctate matte spot lateral to lateral ocellus.

Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i<1d); mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure*. Labral apex with pair of small denticles preceded by submedial pair of small denticles and separated by shallow concavity. Frontal keel not strongly raised. Scape with greatest length 1.7 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5–2 MOD at its terminal (difficult to see in the *E. flavofasciatus* lectotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin (L) less than half as long as mesoscutellar width (W) (L/W ratio = 0.4) and tip not extending beyond midlength of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 1/3 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.2); S3–S5 with much longer coppery to silvery subapical hairs, which individually are often darker apically; pygidial plate unusually narrow (*Triepeolus*-like) and apically rounded, with large deep punctures closely clustered.

**Distribution:** Mexico, excluding the Baja California Peninsula, and southwestern United States to central America (Fig. 48).

**Ecology.** HOST RECORDS: The host species of *E. flavofasciatus* is/are presently unknown.

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Heterotheca subaxillaris* and *Vicia* L. (Leguminosae).

**Discussion.** Smith (1879) described *E. flavofasciatus* from both sexes, represented by two syntypes (one female and one male) deposited at the NHMUK. Both specimens were examined, and the female is herein designated as the lectotype because it is in better condition, because

most *Epeolus* spp. are represented by female name-bearing types, and because Smith (1879) provided a more complete description of the female. The male syntype at the NHMUK is herein designated as the lectoallotype. Cockerell (1907) described this species under the name *Triepeolus agaricifer*, which Rightmyer (2008) synonymized under *E. flavofasciatus*. I have examined the male holotype specimen of *T. agaricifer*, and agree with Rightmyer's treatment. Two specimens (both males) were barcoded, one of which is from Southeast Arizona, USA (nearer the type locality of *T. agaricifer*: Beulah, New Mexico, USA) and the other is from Jalisco, Mexico (nearer the type locality of *E. flavofasciatus*: Oaxaca, Mexico), and both were assigned the same BIN. Brumley also described this species under the manuscript name *Epeolus artus* [*nomen nudum*] in 1965.

There is some intraspecific variation in the pubescence on the metanotum, which ranges from entirely yellow to medially or mostly black, and T1, in which the apical fascia is either complete or interrupted medially, with differences not conforming to any discernable geographic pattern. Based on examined records, the range of this species appears to be quite continuous from the American Southwest to Central America.

Among the examined specimens of this species is one that appears to be the first known example of bilateral gynandromorphism in *Epeolus* (see Material studied). Descriptions and images of the aberrant features exhibited by the specimen are published separately (Onuferko 2018).

**Material studied. Type material.** Primary: Mexico: **Oaxaca:** (*E. flavofasciatus* lectotype ♀ [NHMUK, catalog number: 010812212]).

USA: **New Mexico:** Beulah, viii.????, T.D. Cockerell (*T. agaricifer* holotype ♂ [USNM, catalog number: 534034]).

Secondary: Mexico: **Oaxaca:** (*E. flavofasciatus* lectoallotype ♂ [NHMUK, catalog number: 010812250]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACZ9233. Specimens examined and sequenced.—Mexico: **Jalisco:** 8 km N Atemajac de Brizuela, 08.x.2008, L. Packer (1♂, PCYU).

USA: **Arizona:** vic. Hannagan Meadow (33.6300° N; 109.3200° W) (Greenlee County), 19-20.vii.1998, B. Harris (1♀, LACM).

**Non-barcoded material examined.** Guatemala: **Escuintla:** Volcán Pacaya, 30.xi.1975, S.W.T. Batra (1♀, USNM).

Mexico: **Chiapas:** San Cristóbal de las Casas, 29.v.1969, W.R.M. Mason (1♀, CNC); **Durango:** Coyotes (Durango Dist.), 08.viii.1947, D. Rockefeller Exp. Michener (1♀, BBSL); Navíos (26 mi E El Salto), 02.viii.1964, L.A. Kelton (1♀, CNC); **Michoacán:** 17 mi N Hidalgo, 29.vii.1962, Univ. Kans. Mex. Expedition (2♀, KUNHM); Hidalgo, 12.vii.1963, F.D. Parker and L.A. Stange (1♂, UCBME); **Morelos:** 10 mi N Cuernavaca, 15.viii.1954, Univ. Kans. Mex. Expedition (1♀, KUNHM); **Sinaloa:** Las Palmitas, 13.ix.1977, E.I. Schlinger (2♀, EMEC); **Tlaxcala:** 8 mi WNW Apizaco, 18.vi.1961, Univ. Kans. Mex. Expedition (1♀, KUNHM).

USA: **Arizona:** Catalina Mountains (19 HkHy), 25.vii.1954, G.D. Butler (1♂, KUNHM); Catalina Mountains (24 HkHy), 26.vii.1954, G.D. Butler (1♂, KUNHM); Catalina Mountains (25 HkHy), 14.viii.1954, G. Bohart and G. Butler (1♂, KUNHM); Catalina Mountains (26 HkHy), 14.viii.1954, G. Bohart and G. Butler (1♂, KUNHM), 25.viii.1954, G.D. Butler (1♀, BBSL), 25.viii.1954, G.D. Butler (1♀, KUNHM); Flagstaff (Coconino County), 25.vii.1952, M. Cazier, W. Gertsch, and R. Schrammel (1 chimera, AMNH); Grand Canyon, 19.viii.??39 (1♀, BBSL); Mount Graham (Graham County), 29.viii.1995, J.G. Rozen and S.A. Budick (1♀, AMNH); Pinaleno Mountains (Graham County), 22.viii.1989, Rozen, Foster, and Brewster (1♀, AMNH); Ramsey Canyon (Huachuca Mountains, Cochise County), 1954, W.M. Mann (2♂, USNM); Rose Peak (30 mi N Clifton, Greenlee County), 16.viii.1964, C.D. Michener (1♂, KUNHM); San Francisco Mountains (Flagstaff, Coconino County), 15.viii.1934, E.L. Bell (1♀, AMNH); Santa Catalina Mountains (Pima County), J.L. Neff (1♂, LACM); **New Mexico:** Sapello Canyon (San Miguel County), 26.vii.??02 (1♂, USNM), 27.vii.??02 (1♀, USNM), 31.vii.-01.viii.1963, T.C. Emmel (1♀, LACM); **Texas:** Big Bend National Park (Brewster County), 14.viii.1976, R.T. Ross (1♂, UCBME).

**23. *Epeolus floridensis* Mitchell, 1962**

Figs 49, 50, & 97B

*Epeolus floridensis* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 446 (♀).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. floridensis* apart from all other North American *Epeolus*: the axilla is large, with the tip extending as far back as or beyond the posterior margin of the mesoscutellum, dilated laterally, and like the mesoscutellum ferruginous; the mesopleuron is closely (i≤1d) and evenly punctate; T1 is (with few exceptions) ferruginous and with a distinct, although sometimes medially-interrupted, basal fascia; the mesoscutum and metasomal terga have bands of pale gray to white short appressed setae; at least the T1–T3 apical fasciae are distinctly interrupted medially; and the pseudopygidial area of the female is lunate with the apex <2 × the medial length. *Epeolus floridensis* is similar to *E. howardi*, but in *E. howardi* the mesoscutum and metasomal terga have bands of bright or pale yellow short appressed setae and the metasomal terga (including T1) are black. *Epeolus floridensis* is also similar to *E. packeri*, but in *E. packeri* the T1 basal fascia is absent or reduced to a pair of small patches of pale tomentum, the metasomal terga (including T1) are black, and the pseudopygidial area of the female is lunate with the apex >2 × the medial length.

**Redescription.** FEMALE: Length 7.5 mm; head length 2.1 mm; head width 2.7 mm; fore wing length 5.5 mm.

*Integument coloration.* Black in part, at least partially ferruginous on mandible, labrum, clypeus, antenna, pronotal collar, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, metanotum, mesopleuron, metapleuron, propodeum, legs, T1, T5, pygidial plate, and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth slightly lighter than mandibular apex. Antenna brown and orange in part. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum almost entirely reddish brown. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale gray short appressed setae. Mesoscutum with paramedian band. Mesopleuron sparsely hairy, but tomentum moderately dense along margins. Metanotum with tomentum uninterrupted, uniformly off white. T1 with

discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally by few sparsely scattered pale hairs. T1–T4 with apical fasciae interrupted medially and somewhat broader laterally, T2 with fascia without anterolateral extensions of tomentum. T5 with two patches of pale tomentum lateral to and contacting pseudopygidial area. T5 with pseudopygidial area lunate, its apex less than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Upper paraocular and frontal areas, and vertexal area with punctures equally dense. Impunctate spot lateral to lateral ocellus absent in holotype, but shiny spot present in non-type specimens. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d), the interspaces shining; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i=1–2d), evenly distributed on disc; the interspaces shining somewhat.

*Structure.* Preapical tooth inconspicuous, blunt and obtuse. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.6). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5 MOD at its terminal (difficult to see in holotype; described from non-type specimens). Mesoscutellum weakly bigibbous. Axilla large, its lateral margin (L) more than half as long as mesoscutellar width (W) (L/W ratio = 0.6) and tip extending as far back as apex of horizontal dorsal portion of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 1/3 the medial length of axilla; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: upper paraocular area very finely and sparsely punctate in part, the interspaces shining; F2 shorter, but still longer than wide (L/W ratio = 1.3); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered basomedially and sparser apically and laterally, with the interspaces shining.

**Distribution:** Florida peninsula (Fig. 50).

**Ecology.** HOST RECORDS: The host species of *E. floridensis* is/are presently unknown.

FLORAL RECORDS: Mitchell (1962) indicated a floral association with *Eriogonum tomentosum* Michx. (Polygonaceae). Labels of examined voucher specimens further indicate associations with *Licania michauxii* Prance (Chrysobalanaceae), *Ptilimnium capillaceum* (Michx.) Raf. (Apiaceae), and *Sabal etonia* Swingle ex Nash (Arecaceae).

**Discussion.** *Epeolus floridensis* exhibits very little intraspecific morphological variation. However, one specimen was observed in which T1 is as dark as the remaining terga rather than bright ferruginous, the usual state. Also, in some males the upper paraocular area has comparatively fewer punctures than in females while in other specimens punctures are similarly dense between the sexes. Based on examined records, adults of *E. floridensis* appear to be most active in spring, although Mitchell (1962) lists some paratypes that were collected in mid-July.

**Material studied. Type material.** Primary: USA: **Florida:** Arcadia (DeSoto County), 27.iv.1955, H.E. and M.A. Evans (holotype ♀ [CUIC, catalog number: 00015349]).

Secondary: USA: **Florida:** Arcadia (DeSoto County), 27.iv.1955, H.E. and M.A. Evans (allotype ♂ [CUIC, catalog number: 00015348]), 27.iv.1955, H.E. and M.A. Evans (paratypes 1♀, 1♂, NCSU).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACZ9059. Specimens examined and sequenced.—USA: **Florida:** Archbold Biological Station (Highlands County), 28.iv.-18.v.2008, S.M. Paiero (1♀, 1♂, DEBU); Lake Placid (Highlands County), 17.v.2014, S. Lenberger (1♀, FSCA).

**Non-barcoded material examined.** USA: **Florida:** Archbold Biological Station (27.1838° N; 81.3532° W) (Highlands County), 28.v.2010, M. Deyrup (1♀, ABS); Lake Wales Ridge State Forest (27.6611° N; 81.3964° W) (Polk County), 30.iv.2009, M. Deyrup, A. May, and H. Otte (1♀, ABS); Lake Wales Ridge State Forest (27.6933° N; 81.4279° W) (Polk County),

30.iv.2009, M. Deyrup, A. May, and H. Otte (1♂, ABS); Lake Wales Ridge State Forest (27.6915° N; 81.4282° W) (Polk County), 06.v.2009, M. Deyrup, A. May, and H. Otte (1♀, ABS); N FWC Carter Creek (27.5313° N; 81.4104° W) (Highlands County), 15.v.2010, J. Dunlap, M. and N. Deyrup, and K. Dearborn (1♂, ABS); Saddle Blanket Lakes (27.6696° N; 81.5758° W) (Polk County), 07.v.2009, M. Deyrup (1♂, ABS); Saddle Blanket Lakes (27.6716° N; 81.5759° W) (Polk County), 08.v.2009, M. Deyrup, A. May, and H. Otte (1♀, ABS); Walk-In-The-Water State Forest (27.7613° N; 81.4877° W) (Polk County), 29.v.2010, M. Deyrup (1♀, ABS).

**24. *Epeolus gibbsi* new species**

Figs 3D, 51, 52, 96C, & 97F

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. gibbsi* apart from all other North American *Epeolus*: the mandible has a blunt, obtuse preapical tooth; in females, F2 is less than 1.2 × as long as wide; the axilla does not attain the midlength of the mesoscutellum but the free portion is distinctly hooked, with the tip unattached to the mesoscutellum for more than 1/3 of the entire medial length of the axilla; the mesopleuron is closely and evenly punctate (i≤1d), with the interspaces shining and punctures similar in size; the legs are usually darker, at least from the metacoxa to metatibia; the metasomal terga have rather fine punctures; S4 and S5 of the male have long curved coppery to silvery subapical hairs; and the pseudopygidial area of the female is distinctly campanulate with the apex <2 × the medial length and in contact with two large patches of pale tomentum (one on each side [the two are parallel to each other]) throughout its length. *Epeolus gibbsi* most closely resembles *E. ilicis* and *E. inornatus*, but in males of the latter S4 and S5 have short straight subapical hairs and in both *E. ilicis* and *E. inornatus* the mandible is simple, and in females of both species F2 is more than 1.2 × as long as wide and the pseudopygidial area is not in contact with two large patches of pale tomentum (one on each side) throughout its length (in contact only at apex, diverging basally).

**Description.** FEMALE: Length 7.3 mm; head length 1.9 mm; head width 2.5 mm; fore wing length 5.8 mm.

*Integument coloration*. Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, and legs. Mandible with apex darker than all but extreme base; preapical tooth lighter than mandibular apex (difficult to see in holotype; described from paratype). Antenna dark brown except scape and F1 reddish brown in part. Pronotal lobe dark brown to black. Tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence*. Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron densely hairy, except for two sparsely hairy circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted except for median bare patch in posterior half, uniformly off white. T1 with median elliptical verging on semicircular discal patch. T1 and T2 with apical fasciae interrupted medially, those of T2 and T3 somewhat broader laterally, T2 with fascia with anterolateral extensions of sparser tomentum. T3 and T4 with fasciae complete. T5 with two large patches of pale tomentum parallel to and contacting pseudopygidial area throughout its length. T5 with pseudopygidial area campanulate, its apex less than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~1/3 MOD.

*Surface sculpture*. Punctures dense. Labrum with larger punctures than clypeus, but punctures of both equally dense (i<1d). Impunctate spot lateral to lateral ocellus absent in holotype, but shiny spot present in some paratypes. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate (i≤2d). Mesopleuron with ventrolateral half densely punctate (i≤1d), the interspaces shining; mesopleuron with punctures similar in size and more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i=1–2d), evenly distributed on disc; the interspaces shining somewhat.

*Structure*. Preapical tooth blunt and obtuse. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.8 × greatest width. F2 not noticeably longer than wide (L/W ratio = 1.1). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1 MOD at its terminal (difficult to

see in holotype; described from paratype). Mesoscutellum strongly bigibbous. Axilla small to intermediate in size, its lateral margin (L) less than half as long as mesoscutellar width (W) (L/W ratio = 0.4) and tip attaining midlength of mesoscutellum; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, as long as wide (L/W ratio = 1.0); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered.

**Etymology.** This species is named after its discoverer, Prof. Jason Gibbs, who collected the specimen herein designated as the holotype, recognized it as an unusual find, and brought his discovery to my attention.

**Distribution:** Upper midwest and adjacent Canada (Fig. 52).

**Ecology.** HOST RECORDS: The holotype of *E. gibbsi* was collected in an area where *Colletes brevicornis* and *C. kincaidii* were in abundance, the latter of which is likely associated with *E. minimus*, which was also present at the site, as was *E. ainsliei* and its tentative host *C. susannae* (J. Gibbs, personal communication, 2017).

FLORAL RECORDS: Unknown.

**Discussion.** What Romankova (2004) identified as *E. ilicis*, which constituted a new record of that species in Canada, might actually be *E. gibbsi* and/or *E. inornatus*. Unfortunately, the vouchered material from that study (three specimens from Ontario) cannot be traced, so the presence of *E. ilicis* in Canada has not been confirmed in the present study. *Epeolus ilicis* has been reported from the New England states, though the only examined specimen from that region (a male from Massachusetts) that has been identified as *E. ilicis* (by Richard L. Brumley) appears to actually be *E. inornatus* based on the very short straight subapical hairs on S4 and S5. In Canada, *E. gibbsi* is only confirmed from southern Manitoba, so the specimens from southern

Ontario studied by Romankova could represent any of the three species. The key presented in Onuferko (2017) still works for *E. ilicis*, but can also lead to *E. gibbsi* and *E. inornatus* with the modifications presented in Suppl. material 3 starting at couplet 4. Presently, only a single 422 bp sequence is available for *E. ilicis* (a male specimen from Florida, USA), which clusters with sequences of *E. zonatus* (Suppl. material 2), and all were assigned the same BIN. In addition to the diagnostic morphological features that separate *E. gibbsi* from other similar species (notably *E. erigeronis*, *E. ilicis*, and *E. inornatus*, for which only partial sequences 394 to 422 bp in length are available), the status of *E. gibbsi* as a separate species is supported by a separate BIN and large barcode sequence divergence (4.7%) from its nearest neighbor, *E. glabratus*. Based on the few known records, adults of *E. gibbsi* appear to be active in late spring/early summer.

**Material studied. Type material.** Primary: Canada: **Manitoba:** Spruce Woods Provincial Park (49.6630° N; 99.2790° W) (Spirit Sands, Division 7), 07.vii.2017, J. Gibbs and Nozoe (holotype ♀ [CCDB-30345 D02], JBWM).

Secondary: USA: **Wisconsin:** Two Rivers, 26.vi.1911 (allotype ♂, CUM), 26.vi.1911 (paratypes 1♀, 6♂, CUM).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ADI6791. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**25. *Epeolus glabratus* Cresson, 1878**

Figs 53, 54, & 93B

*Epeolus glabratus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 90 (♂).
*Pyrrhomelecta glabrata* Ashmead, 1899. Trans. Am. Entomol. Soc. 26: 66.

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. glabratus* apart from all other North American *Epeolus* except *E. lectoides*: the axilla is elongate, extending well beyond the midlength of the mesoscutellum but not as far back as its posterior margin, and the free

portion is distinctly hooked; the mesopleuron has sparser punctures ventrolaterally (most i>1d) than in upper half, with the interspaces shining; the metasomal terga have minute, shallow punctures; T2–T4 are medially bare; and the pseudopygidial area of the female is distinctly campanulate with the apex <2 × the medial length. Whereas in *E. lectoides* the pronotal collar is black, as are sometimes the axilla and mesoscutellum, and the metasomal terga are black and fasciate, in *E. glabratus* the pronotal collar, axilla, mesoscutellum, and discs of T1 and T2 are ferruginous and the pale pubescence on the metasomal terga are commonly reduced to discrete lateral patches.

**Redescription.** MALE: Length 8.4 mm; head length 1.8 mm; head width 2.5 mm; fore wing length 7.9 mm.

*Integument coloration.* Black in part, at least partially ferruginous on mandible, labrum, clypeus, antenna, pronotal collar, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, mesopleuron, metapleuron, legs, T1, T2, pygidial plate, and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth lighter than mandibular apex (difficult to see in holotype because mandible closed; described from non-type specimens). Antenna brown except scape, pedicel, and F1 extensively orange. F2 with orange spot basally. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane dusky subhyaline, slightly darker at apex. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron sparsely hairy, but tomentum dense ventrally as well as between two sparsely hairy patches (one beneath base of fore wing (hypoepimeral area), a larger circular patch occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted except for median bare patch in posterior half, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally. T1 with basal and apical fasciae and T2–T4 with apical fasciae widely separated medially, the apical fasciae reduced to pairs of small patches somewhat broader laterally; T2 with fascia without anterolateral extensions of tomentum, although few sparsely scattered pale hairs present. Remaining metasomal terga mostly hidden in

holotype, but T5 and T6 with complete or narrowly interrupted fasciae in non-type specimens. S4 and S5 with long coppery to silvery subapical hairs.

*Surface sculpture.* Punctures dense, but those of head and mesosoma sparser in some areas, larger, deep, and distinct. Labrum with larger punctures than clypeus, but punctures of both equally dense (i<1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla very coarsely and densely punctate; the interspaces shining. Tegula densely punctate (i≤2d). Mesopleuron mostly with denser (i≤1d) punctures in upper half than ventrolateral half (i>1d), the interspaces shining. Metasomal terga with punctures very fine, dense (i≥1d), somewhat evenly distributed on disc; the interspaces shining somewhat.

*Structure.* Preapical tooth blunt and obtuse. Labrum with pair of small subapical denticles, each preceded by small discrete longitudinal ridge. Frontal keel not strongly raised. Scape with greatest length 1.7 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.3). Preoccipital ridge not joining hypostomal carina, from which it is separated by less than 1 MOD at its terminal (difficult to see in holotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla large, its lateral margin (L) more than half as long as mesoscutellar width (W) (L/W ratio = 0.6) and tip extending well beyond midlength of mesoscutellum but not as far back as its posterior margin; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin relatively straight and with tip carinate. Fore wing with three submarginal cells. Pygidial plate mostly hidden in holotype, but apically rounded, with large deep punctures more or less evenly spaced throughout with the interspaces shining in non-type specimens.

FEMALE: Description as for male except for usual secondary sexual characters and as follows: F2 even longer than wide (L/W ratio = 1.5); T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area present only in female; T5 with pseudopygidial area campanulate, its apex less than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum; S4 and S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~1/3 MOD); pygidial plate apically truncate, with small, denser punctures.

**Distribution:** Florida and coastal Georgia (Fig. 54).

**Ecology.** HOST RECORDS: The host species of *E. glabratus* is/are presently unknown.

FLORAL RECORDS: Mitchell (1962) indicated a floral association with *Vicia*. Labels of examined voucher specimens further indicate associations with *Coreopsis* L., *Hyptis mutabilis* (Rich.) Briq. (Lamiaceae), *Ilex glabra*, *Pluchea odorata* (L.) Cass. (Compositae), *Polygonella myriophylla* (Small) Horton (Polygonaceae), *Richardia brasiliensis* Gomes (Rubiaceae), *Serenoa repens* (W. Bartram) Small (Arecaceae), *Spermacoce verticillata* L., and *Verbena brasiliensis* Vell.

**Discussion.** Sequenced specimens of *E. glabratus* share the same BIN as those of *E. lectoides*. There is virtually no divergence (<1%) between the barcode sequences of the two species, but the morphological differences are pronounced. Structurally, *E. glabratus* and *E. lectoides* are identical, but in *E. glabratus* the pronotal collar, axilla, mesoscutellum, and discs of T1 and T2 are ferruginous, whereas in *E. lectoides* at least the pronotal collar and metasomal terga are entirely black. *Epeolus glabratus* appears to be restricted to Florida and parts of Georgia, and the prevalence of red integument coloration among Florida Hymenoptera is a well-known unexplained phenomenon (Deyrup and Eisner 2003). Except in some examined specimens from Georgia, in *E. glabratus* the metasomal fasciae are lacking; the pale pubescence is instead reduced to discrete lateral patches. By contrast, in *E. lectoides* the metasomal terga are always fasciate. Although both species inhabit Florida, *E. glabratus* (with red coloration and reduced pubescence on the metasomal terga) appears to be present only on the peninsula whereas *E. lectoides* (with fasciae and black metasomal terga) appears to be restricted to the Florida panhandle. Since the marked abundance of red coloration is coupled with a general loss of pubescence in *E. glabratus*, and since these are features restricted to specimens from a particular geographical region, I have opted to treat *E. glabratus* and *E. lectoides* as heterospecific, despite the lack of evidence of genetic divergence.

**Material studied. Type material.** Primary: USA: **Georgia:** H.K. Morrison (holotype ♂ [ANSP, catalog number: 2230]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAF2273.
Specimens examined and sequenced.—USA: **Florida:** Archbold Biological Station (27.1711° N; 81.3483° W) (Highlands County), 21-26.iv.2011, R.J. Pivar (1♂, DEBU); Archbold Biological Station (Highlands County), 07-13.v.1995, C. Darling (1♀, PCYU); N FWC Carter Creek (27.5313° N; 81.4104° W) (Highlands County), 11.v.2010, J. Dunlap, M. and N. Deyrup, and K. Dearborn (1♂, ABS).

**Non-barcoded material examined.** USA: **Florida:** Archbold Biological Station (Highlands County), 14.iv.1963, J.G and B.L. Rozen (1♀, AMNH); Doyle Conner Bldg (Gainesville, Alachua County), 12.vi.1996, C. Porter (1♀, FSCA), 18.vi.1996, C. Porter (2♀, FSCA), 26.vi.1996, C. Porter (1♂, FSCA); Gainesville (Alachua County), 03-17.vii.1987, BRC Hymenoptera Team (1♀, PCYU), 07.vi.1976, W.H. Pierce (1♀, UCBME), 16.vi.1991, F.J. Santana (1♀, FSCA), 17.vi.1976, W.H. Pierce (1♀, 1♂, UCBME); Lake Alice (29.6442° N; 82.3630° W) (University of Florida, Gainesville, Alachua County), 05.vi.2007, J.S. Ascher and G. Hall (2♀, AMNH); Lake Placid (Highlands County), 17.v.2014, S. Lenberger (1♂, FSCA); Lake Wales Ridge State Forest (27.6611° N; 81.3964° W) (Polk County), 06.v.2009, M. Deyrup, A. May, and H. Otte (1♀, ABS); Naples (Golden Gate Estates Subdivision, Collier County), 25.v.2013, S. Lenberger (1♂, FSCA); Near Wilcox (Gilchrist County), 27.v.1981, C. Porter, L. Stange, and H. Greenbaum (1♀, FSCA); Newberry (Alachua County), 15.vii.1973, E.E. Grissell (1♂, UCBME); Royal Palm Park, 12-18.iv.1923 (1♂, AMNH); San Felasco State Hammock Preserve, 20.v.1977, G.B. Fairchild and H.V. Weems, Jr. (1♂, UCBME); Sarasota (Sarasota County), 31.v.1993, F.J. Santana (2♀, FSCA); U.S. Highway 41 S Lake City (Columbia County), 19.vi.2014, S. Lenberger (2♀, FSCA); **Georgia:** St Catherines Island (Liberty County), 10-15.v.1991, E. Quinter and A. Sharkov (1♂, AMNH); St Catherines Island (South Beach, Liberty County), 27.vi.1974, R.O. Schuster and E.C. Teftner (1♀, UCBME).

**26. *Epeolus howardi* Mitchell, 1962**

Figs 55 & 56

*Epeolus howardi* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 447 (♀).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. howardi* apart from all other North American *Epeolus*: the axilla is large, with the tip extending as far back as or beyond the posterior margin of the mesoscutellum, dilated laterally, and like the mesoscutellum ferruginous; the mesopleuron is closely (i≤1d) and evenly punctate; the metasomal terga are black; T1 has a distinct, although sometimes medially-interrupted, basal fascia; the mesoscutum and metasomal terga have bands of bright or pale yellow short appressed setae; at least the T1–T3 apical fasciae are distinctly interrupted medially; and the pseudopygidial area of the female is lunate with the apex <2 × the medial length. *Epeolus howardi* most closely resembles *E. andriyi* and *E. floridensis*, but in *E. andriyi* the axillae are shorter, not extending as far back as the posterior margin of the mesoscutellum, and in *E. floridensis* the mesoscutum and metasomal terga have bands of pale gray to white short appressed setae and T1 is (with few exceptions) ferruginous. *Epeolus howardi* is also similar to *E. scutellaris*, but in *E. scutellaris* the T1–T3 apical fasciae are complete or only very narrowly interrupted medially, and the pseudopygidial area of the female is lunate with the apex >2 × the medial length.

**Redescription.** FEMALE: Length 8.6 mm; head length 2.2 mm; head width 2.9 mm; fore wing length 6.0 mm.

*Integument coloration.* Black in part, at least partially ferruginous on mandible, labrum, clypeus, antenna, pronotal collar, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, metanotum, mesopleuron, legs, T1, pygidial plate, and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth slightly lighter than mandibular apex. Antenna brown and orange in part. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum reddish brown along lateral margin and with pair of reddish-brown markings near posterior margin between midline and parapsidal line. Wing membrane dusky subhyaline, slightly darker at apex. Legs more extensively reddish orange than brown or black. T1 dark in general, not contrasting strongly with remaining metasomal terga, but reddish brown laterally.

*Pubescence.* Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron sparsely hairy, but tomentum moderately dense along margins.

Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally by few sparsely scattered pale hairs. T1–T4 with apical fasciae interrupted medially and narrowed before becoming somewhat broader laterally, T2 with fascia without anterolateral extensions of tomentum. T5 with two patches of pale tomentum lateral to and contacting pseudopygidial area. T5 with pseudopygidial area lunate, its apex less than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger punctures than clypeus, but punctures of both equally dense (i<1d). Upper paraocular area sparsely punctate in part, the interspaces shining. Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with denser (i≤1d) punctures in upper half than ventrolateral half (i≤2d), the interspaces shining. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc; the interspaces shining somewhat.

*Structure.* Preapical tooth inconspicuous, blunt and obtuse. Labrum with pair of small subapical denticles, each preceded by small discrete longitudinal ridge. Frontal keel not strongly raised. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.7). Preoccipital ridge not joining hypostomal carina, from which it is separated by less than 1 MOD at its terminal. Mesoscutellum weakly bigibbous. Axilla large, its lateral margin (L) more than half as long as mesoscutellar width (W) (L/W ratio = 0.7) and tip extending beyond apex of horizontal dorsal portion of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.3); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

**Distribution:** Mid-Atlantic states to Texas (Fig. 56).

**Ecology.** HOST RECORDS: According to Mitchell (1962), *Colletes howardi* Swenk is the suspected host of *E. howardi*.

FLORAL RECORDS: Mitchell (1962) indicated a floral association with *Dalea pinnata* (J.F.Gmel.) Barneby. Labels of examined voucher specimens further indicate associations with *Heterotheca subaxillaris* ssp. *latifolia* (Buckley) Semple, *Symphyotrichum drummondii* var. *texanum* (E.S. Burgess) G.L. Nesom, and *Xanthisma texanum* DC. (Compositae).

**Discussion.** *Epeolus howardi* is a southeastern species that appears to be uncommon, or at least uncommonly collected. In general, there is little morphological variation among examined specimens except in integument coloration; the mesoscutum and mesopleuron range from varying degrees of ferruginous to entirely black, with differences not conforming to any discernable geographic pattern. Based on known records, adults of *E. howardi* are active in late summer and much of autumn.

**Material studied. Type material.** Primary: USA: **North Carolina:** Southern Pines, 30.ix.1951, T.B. Mitchell (holotype ♀ [USNM, catalog number: 534046]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ADK0941. Specimens examined and sequenced.—USA: **Maryland:** Denton (38.9196° N; 75.8273° W) (Caroline County), 19.viii.2012, S. Westre (1♂, BIML).

**Non-barcoded material examined.** USA: **Texas:** Austin (Travis County), 27.x.1981, J.L. Neff (1♀, CTMI); Brackenridge Field Laboratory (Austin, Travis County), 02.xi.1992, J.L. Neff (1♀, CTMI); Brazos County, 24.x.1960, A.H. Alex (1♀, USNM); Dallas, 15.x.??05, F.C. Bishopp (1♀, USNM); Sayersville (Bastrop County), 20.ix.1998, J.L. Neff (1♀, CTMI).

**27. *Epeolus ilicis* Mitchell, 1962**

Figs 3E, 57, 58, 92F, 97G, & 100A

*Epeolus ilicis* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 448 (♀).

*Epeolus vernalis* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 455 (♀), **syn. n.**
*Epeolus weemsi* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 455 (♂), **syn. n.**

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. ilicis* apart from all other North American *Epeolus* except *E. erigeronis* and *E. inornatus*: the mandible is simple; the axilla does not attain the midlength of the mesoscutellum but the free portion is distinctly hooked, with the tip unattached to the mesoscutellum for more than 1/3 of the entire medial length of the axilla; the pronotal collar and metasomal terga are black; the metasomal terga have rather fine punctures; and the pseudopygidial area of the female is distinctly campanulate with the apex <2 × the medial length and not in contact with two large patches of pale tomentum (one on each side) throughout its length (in contact only at apex, diverging basally). *Epeolus ilicis* is most similar to *E. inornatus*, and in both species the mesopleuron has punctures that are similar in size and shiny interspaces that are commonly equal to the puncture diameters. By contrast, in *E. erigeronis* the punctures are more variable in size, with many smaller punctures among large ones, and most interspaces are narrower such that the surface appears to be very coarsely and densely rugose-punctate. Whereas in *E. inornatus* the legs (and sometimes the pronotal lobe and tegula) are usually darker, at least from the metacoxa to metatibia, the dorsum of the mesosoma and metasoma have gray short appressed setae, and S4 and S5 of the male have short straight subapical hairs, in *E. ilicis* the pronotal lobe and legs are more extensively reddish orange than brown or black (at least the anterior surface of the metatibia and metatarsus are the same reddish orange color), the dorsum of the mesosoma and metasoma have gray but also usually some pale yellow short appressed setae, and S4 and S5 of the male have long curved coppery to silvery subapical hairs. *Epeolus ilicis* is also similar to *E. gibbsi*, but in *E. gibbsi* the mandible has a blunt, obtuse preapical tooth; in females F2 is less than 1.2 × as long as wide (it is more than 1.2 × as long as wide in female *E. ilicis*); and the pseudopygidial area of the female is in contact with two large patches of pale tomentum (one on each side [the two are parallel to each other]) throughout its length.

**Redescription.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Southeastern United States (Fig. 58).

**Ecology.** HOST RECORDS: Rozen (1989) described first instar *E. ilicis* based on two larvae recovered from the nest of *Colletes brimleyi* Mitchell on St. Catherines Island in Georgia, USA, from where conspecifics of the former have been recorded (see Material studied).

FLORAL RECORDS: Onuferko (2017) lists associations with five plant genera based on Mitchell (1962) and a record on Discover Life (Ascher and Pickering 2017 [then 2016]). Since the discovery of *E. inornatus*, a cryptic species very similar to *E. ilicis* whose name applies to at least one of Mitchell's paratypes of *E. ilicis* (see Material studied under *E. inornatus*), my taxon concept of *E. ilicis* has changed. As a result, I have only been able to determine that records of *Ilex glabra* and *Prunus angustifolia* Marshall (Rosaceae), taken from the collection labels of the holotypes of *E. ilicis* and *E. weemsi* respectively, are associated with what is here understood to be the true *E. ilicis*.

**Discussion.** Both the holotype of *E. ilicis* and the holotype of *E. vernalis* were examined, and the two appear to be the same species. In Mitchell's (1962) key, the two species were differentiated on the basis of whether or not (and if so to what degree) the metasomal fasciae are interrupted medially, but the T1–T3 apical fasciae are interrupted medially (those of T1 and T2 are somewhat more widely separated medially) in both holotype specimens and the T4 fascia is complete in the *E. ilicis* holotype and only very narrowly interrupted in the *E. vernalis* holotype. Moreover, the type locality is the same for both (Holly Shelter [Pender County], North Carolina, USA), and the two specimens were collected only 12 days apart.

Presently, only a single 422 bp sequence is available for *E. ilicis* (a male specimen from Florida, USA), which clusters with sequences of *E. zonatus* (Suppl. material 2), and all were assigned the same BIN. The Florida specimen is most similar to the holotype of *E. weemsi*, which Mitchell (1962) described before noting that it might be the male of *E. vernalis*. In both the sequenced specimen and *E. weemsi* holotype, S4 and S5 have long curved coppery to silvery subapical hairs, which are absent in the very similar *E. inornatus* but present in all other North American male *Epeolus*. Whereas I have opted to treat *E. ilicis* and *E. zonatus* as heterospecific based on remarkably consistent differences in integument coloration coupled with a general loss of pubescence in *E. zonatus*, despite the apparent lack of evidence of genetic divergence, the

extremely subtle differences in integument coloration and pubescence among the holotypes of *E. ilicis*, *E. vernalis*, and *E. weemsi* seem to fall within the range of intraspecific variation, and therefore *E. vernalis* and *E. weemsi* are herein synonymized under *E. ilicis*. Although the three names were published simultaneously, priority of the name should be given to *E. ilicis* because the holotype is in the best condition (those of *E. vernalis* and *E. weemsi* have broken antennae and in the latter much of the pubescence is discolored or rubbed off), it is female and most *Epeolus* spp. were described from female name-bearing types (the holotype of *E. weemsi* is male), and because an allotype and paratypes were designated for *E. ilicis* but not *E. vernalis* or *E. weemsi*. This species appears to be quite common in the Southeastern United States, where it may be confused with *E. erigeronis* or *E. inornatus*.

**Material studied. Type material.** Primary: USA: **Florida:** Alachua County, 23.ii.1957, H.V. Weems, Jr. (*E. weemsi* holotype ♂, FSCA); **North Carolina:** Holly Shelter (Pender County), 30.v.1950, T.B. Mitchell (*E. ilicis* holotype ♀ [USNM, catalog number: 534048]), 18.v.1950, T.B. Mitchell (*E. vernalis* holotype ♀ [USNM, catalog number: 534607]).

Secondary: USA: **Georgia:** Fort Gordon (Richmond County), 25.iv.1959, R.R. Snelling (paratype ♂, NCSU); **South Carolina:** McClellanville, 12.v.??44, H.K. Townes (paratype ♂, NCSU), 19.v.??44, H. and G. Townes (paratype ♂, NCSU).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACM5887. Specimens examined and sequenced.—USA: **Florida:** Apalachicola National Forest (30.3291° N; 84.5052° W) (Forest Rd 366, Leon County), 15-20.v.2005, A. Deans, S. Joshi, and D. Murray (1♂, AMNH).

**Non-barcoded material examined.** USA: **Alabama:** Bon Secour National Wildlife Refuge (Baldwin County), 05-07.v.1994, S.A. Marshall (1♀, DEBU); **Florida:** A.T. Slosson (1♀, AMNH); 3 mi NW Sopchoppy (near Sopchoppy River, Wakulla County), 19.iv.1979, G.B. Fairchild (3♀, FSCA); Blackwater River State Forest (4 mi N Munson, Santa Rosa County), 12.vi.1988, L. Stange and J. Wiley (1♀, FSCA); Destin (Okaloosa County), 17.v.1969, H.V. Weems, Jr. (1♀, FSCA); St. Andrews State Park (Bay County), 05-07.v.1987, L. Stange and J. Wiley (2♀, FSCA), 06-07.v.1987, L. Stange and J. Wiley (1♀, 1♂, FSCA); Suwannee River

State Park, 13-25.iv.1977, J.R. Wiley (1♂, FSCA); Torreya State Park (Liberty County), 18.v.1970, H.V. Weems, Jr. (1♀, FSCA); **Georgia:** St. Catherines Island (Liberty County), 24-28.iv.1972, Thompson and Picchi (1♂, AMNH), 10-14.iv.1991, J.G. Rozen, E. Quinter, and A. Sharkov (1♀, AMNH); **South Carolina:** Hunting Island State Park (Beaufort County), 08.iv.1963, J.G. and B.L. Rozen (1♂, AMNH).

**28. *Epeolus inornatus* new species**

Figs 59, 60, 92G, 93C, 96D, & 100B

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. inornatus* apart from all other North American *Epeolus* except *E. erigeronis* and *E. ilicis*: the mandible is simple; the axilla does not attain the midlength of the mesoscutellum but the free portion is distinctly hooked, with the tip unattached to the mesoscutellum for more than 1/3 of the entire medial length of the axilla; the pronotal collar and metasomal terga are black; the metasomal terga have rather fine punctures; and the pseudopygidial area of the female is distinctly campanulate with the apex <2 × the medial length and not in contact with two large patches of pale tomentum (one on each side) throughout its length (in contact only at apex, diverging basally). *Epeolus inornatus* is most similar to *E. ilicis*, and in both species the mesopleuron has punctures that are similar in size and shiny interspaces that are commonly equal to the puncture diameters. By contrast, in *E. erigeronis* the punctures are more variable in size, with many smaller punctures among large ones, and most interspaces are narrower such that the surface appears to be very coarsely and densely rugose-punctate. Whereas in *E. ilicis* the pronotal lobe and legs are more extensively reddish orange than brown or black (at least the anterior surface of the metatibia and metatarsus are the same reddish orange color), the dorsum of the mesosoma and metasoma have gray but also usually some pale yellow short appressed setae, and S4 and S5 of the male have long curved coppery to silvery subapical hairs, in *E. inornatus* the legs (and sometimes the pronotal lobe and tegula) are usually darker, at least from the metacoxa to metatibia, the dorsum of the mesosoma and metasoma have gray short appressed setae, and S4 and S5 of the male have short straight subapical hairs. *Epeolus inornatus* is also similar to *E. gibbsi*, but in *E. gibbsi* the mandible has a blunt, obtuse preapical tooth; in males S4 and S5 have long curved coppery to

silvery subapical hairs, as in *E. ilicis* and all other Nearctic *Epeolus*; in females F2 is less than 1.2 × as long as wide (it is more than 1.2 × as long as wide in female *E. inornatus*); and the pseudopygidial area of the female is in contact with two large patches of pale tomentum (one on each side [the two are parallel to each other]) throughout its length.

**Description.** FEMALE: Length 8.2 mm; head length 1.9 mm; head width 2.6 mm; fore wing length 5.7 mm.

*Integument coloration*. Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, and legs. Mandible with apex darker than all but extreme base. Antenna dark brown except F1 reddish brown in part. Pronotal lobe dark brown to black. Tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs with brown or black more extensive than reddish orange.

*Pubescence*. Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale gray short appressed setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, ventrolateral half nearly bare. Metanotum with tomentum uninterrupted except for median bare patch in posterior half, uniformly off white. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2 with fascia interrupted medially and with faint anterolateral extensions of sparser tomentum. T3 and T4 with fasciae complete. T5 with two large patches of pale tomentum lateral to and contacting pseudopygidial area at apex, diverging from pseudopygidial area basally. T5 with pseudopygidial area campanulate, its apex less than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

*Surface sculpture*. Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d), the interspaces shining; mesopleuron with punctures similar in size and more or less

equally dense throughout. Metasomal terga with punctures very fine, dense (i=1–2d), evenly distributed on disc; the interspaces shining somewhat.

*Structure*. Mandible without preapical tooth. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.9 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin (L) less than half as long as mesoscutellar width (W) (L/W ratio = 0.4) and tip not extending beyond midlength of mesoscutellum; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin relatively straight and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, not noticeably longer than wide (L/W ratio = 1.1); pygidial plate apically rounded, with large deep punctures closely clustered.

**Etymology.** The name is in reference to the grayish pubescence and largely monochromatic dark brown or black integument of this species. From the Latin, “inornatus” (unadorned).

**Distribution:** Mid-Atlantic states to Texas (Fig. 60).

**Ecology.** HOST RECORDS: The host species of *E. inornatus* is/are presently unknown.

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Quercus laevis* Walter (Fagaceae) and *Vaccinium arboreum* Marshall.

**Discussion.** The specimens from Texas, USA that Brumley (1965) identified as *E. ilicis* are probably *E. inornatus*. Although BIN-compliant sequences are presently not available for *E. inornatus*, a single 421 bp sequence is available for a female specimen (the holotype) from East Texas, which does not cluster with the single sequence (422 bp in length) available for what is herein considered to be the true *E. ilicis* (a male specimen from Florida, USA) based on its greater resemblance to the holotype of that species (Suppl. material 2). Instead, the sequence

from the Florida specimen clusters with sequences of *E. zonatus*, which is a visibly different bee, and all were assigned the same BIN. Whereas male *E. inornatus* are unique among *Epeolus* in having very short straight subapical hairs on S4 and S5 instead of the usual long curved coppery to silvery subapical hairs, females are practically indistinguishable from *E. ilicis* in terms of surface sculpture and structure. Although consistent, the features (differences in integument coloration and pubescence) that in combination may be used to distinguish female *E. inornatus* from *E. ilicis* are subtle. Based on known records, adults of *E. inornatus* appear to be most active in spring, the same time of year when adults of *E. ilicis* and *E. zonatus* are active.

**Material studied. Type material.** Primary: USA: **Texas:** Lick Creek Park (College Station, Brazos County), 05-09.iv.2000, M. Buck (holotype ♀ [DEBU, catalog number: 00106728]).

Secondary: USA: **Arkansas:** Magazine Mountain (Logan County), 23.v.1991, J. Powell (paratype ♀, EMEC); **Florida:** Liberty County, 24.iv.1961, H.V. Weems, Jr. (paratype ♂, BBSL); Torreya State Park (Liberty County), 12.v.1968, H.V. Weems, Jr. (paratype ♂, FSCA); **Georgia:** 2 mi SE Blue Ridge (Fannin County), 29.vi.1982, J.B. Whitfield (paratype ♂, EMEC); Rabun Bald (Rabun County), 14.vii.1957, J.G. Chillcott (paratype ♀, CNC); Satolah (Rabun County), 01.vii.1957, J.R. Vockeroth (paratype ♀, CNC), 04.vii.1957, W.R.M. Mason (paratype ♂, CNC); **Massachusetts:** Amherst, spring 1929, L.A. Carruth (paratype ♂, USNM); **North Carolina:** Chestnut Bald (Pisgah National Forest, Haywood County), 02.viii.1957, J.G. Chillcott (paratype ♀, CNC); Highlands, 27.vi.1957, W.R.M. Mason (paratype ♀, CNC), 27.vi.1957, J.R. Vockeroth (paratypes 3♂, CNC), 29.vi.1957, J.R. Vockeroth (paratype ♀, CNC), 25.vi.1957, W.R.M. Mason (paratype ♂, CNC); Horse Cove (Highlands), 27.vi.1957, J.R. Vockeroth (paratype ♂, CNC); Wayah Bald (Macon County), 06.vii.1957, W.R.M. Mason (paratype ♀, CNC); Whiteside Mountain (Highlands), 29.vi.1957, W.R.M. Mason (paratype ♀, CNC); **South Carolina:** Mountain Rest, 14.vi.1957, W.R.M. Mason (paratype ♂, CNC); **Texas:** 2.5 mi S Delhi (29.7730° N; 97.4020° W) (Caldwell County), 19.iv.2007, J.L. Neff and A. Hook (paratype ♀, CTMI); 8 km SE Elkhart (Anderson County), 27.iv.1985, C.D. Michener (paratype ♂, KUNHM); Brackenridge Field Laboratory (Austin, Travis County), 13.v.1988, A. Hook (paratype ♂, CTMI); Lick Creek Park (College Station, Brazos County), 05-09.iv.2000, M. Buck (allotype ♂ [DEBU, catalog number: 00106727]); Stengl Lost Pines Biological Research Station (30.0800° N; 97.1830° W) (Bastrop County), 13.iv.2006, J.L. Neff (paratype ♀, CTMI).

**DNA barcoded material with BIN-compliant sequences.** Unavailable.

**Non-barcoded material examined.** USA: **North Carolina:** Whiteside Mountain (Macon County), 11.vii.1937, T.B. Mitchell (*E. ilicis* paratype ♂, NCSU).

**29. *Epeolus interruptus* Robertson, 1900**

Figs 61 & 62

*Epeolus interruptus* Robertson, 1900. Trans. Acad. Sci. St. Louis 10: 55 (♀).

**Diagnosis.** Unique to *E. interruptus* among North American species of *Epeolus* are each of the following morphological features: the metanotum has a blunt median process and T1 has a wide triangular discal patch with concave lateral sides. *Epeolus interruptus* most closely resembles *E. tessieris* in that the mesoscutum has short paramedian bands; the axilla does not attain the midlength of the mesoscutellum and like the mesoscutellum is ferruginous (although both are occasionally black in *E. interruptus*); the mesopleuron commonly has sparser punctures ventrolaterally than in upper half, with the interspaces shining; and T1–T4 have medially-interrupted metasomal fasciae. However, in *E. tessieris* the metanotum is flat and T1 has a trapezoidal to nearly semicircular discal patch.

**Redescription.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Central and western Canada, east of the Rocky Mountains, to northern Mexico (Fig. 62).

**Ecology.** See Onuferko (2017) for host and floral records. Floral associations are also indicated in Suppl. material 1, which includes a newly discovered association with *Heterotheca villosa* (Pursh) Shinners based on the label of one examined voucher specimen.

**Discussion.** Detailed morphological and taxonomic remarks about this species are given in Onuferko (2017).

**Material studied. Type material.** Primary: USA: **Illinois:** Carlinville (Macoupin County), C.A. Robertson (holotype ♀ [INHS, catalog number: 44384]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACZ9058. Specimens examined and sequenced.—USA: **Arizona:** 3♀, 2♂ (PCYU); **Utah:** 1♂ (BBSL); **Virginia:** 1♀ (CTMI).

**Non-barcoded material examined.** Canada: **Manitoba:** 6♀ (CNC); **Ontario:** 1♀ (CNC).

Mexico: **Baja California:** 1♂ (EMEC); San Vicente, 08.vii.1963, J.D. Birchim (2♀, CAS); **Baja California Sur:** vic.Est. Microondas "Ligüí" (48 km S Loreto), 07.ix.1977, R.R. Snelling (1♀, 1♂, LACM); **Nuevo León:** Cola de Caballo, 18.vi.1975, H.V. Weems, Jr. (1♂, FSCA).

USA: **Arizona:** 2♀, 4♂ (AMNH, PCYU); 4.7 mi SE Portal (Cochise County), 03.ix.1978, R.E. Coville (1♀, EMEC); **California:** Colton, 26-28.v.1917, E.P. Van Duzee (1♂, CAS); **Colorado:** Boulder, 20.vii.1908, S.A. Rohwer (1♂, CAS); Eldorado Springs, 08.vii.1962, U.N. Lanham (1♂, CUM); Roxborough State Park (39.4356° N; 105.0760° W), 12.vi.2000, A.L. Hicks and V. Scott (1♂, CUM); **Idaho:** 5 mi E Harvard, 21.vii.1971, R.M. Bohart (1♂, UCBME); **Iowa:** 1♀ (AMNH); **Louisiana:** 1♂ (USNM); **Michigan:** G. H. Gordon Biological Station (44.0470° N; 85.6670° W) (Lake County), 28.vi.2015, J. Gibbs (1♂, JBWM); **Nebraska:** 1♀ (AMNH); **New Mexico:** 2♂ (BBSL, FMNH); **Texas:** 3♀ (AMNH, CTMI); 30 mi N Uvalde (Uvalde County), 21.vi.1983, W.J. Pulawski (1♂, CAS); McAllen Botanical Gardens (McAllen), 1973, C.C. Porter (1♂, FSCA), 20.iii.1976, C.C. Porter (1♀, FSCA); **Utah:** 1♂ (BBSL).

**30. *Epeolus lectoides* Robertson, 1901**

Figs 63 & 64

*Epeolus lectoides* Robertson, 1901. Can. Entomol. 33: 231 (♀).

*Epeolus semilectus* Cockerell, 1907a. Entomologist 40: 136 (♂).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. lectoides* apart from all other North American *Epeolus* except *E. glabratus*: the axilla is elongate, extending well beyond the midlength of the mesoscutellum but not as far back as its posterior margin, and the free portion is distinctly hooked; the mesopleuron has sparser punctures ventrolaterally (most i>1d) than in upper half, with the interspaces shining; the metasomal terga have minute, shallow punctures; the T2–T4 fasciae are conspicuously narrowed or interrupted medially; and the pseudopygidial area of the female is distinctly campanulate with the apex <2 × the medial length. Whereas in *E. glabratus* the pronotal collar, axilla, mesoscutellum, and discs of T1 and T2 are ferruginous and the pale pubescence on the metasomal terga are commonly reduced to discrete lateral patches, in *E. lectoides* the pronotal collar is black, as are sometimes the axilla and mesoscutellum, and the metasomal terga are black and fasciate. *Epeolus lectoides* is also similar to *E. lectus*, but in *E. lectus* the metasomal terga have coarse, deep punctures and the T2–T4 fasciae are complete and evenly broad.

**Redescription.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Eastern North America (Fig. 64).

**Ecology.** See Onuferko (2017) for host and floral records. Floral associations are also indicated in Suppl. material 1, which includes newly discovered associations with *Aralia spinosa* L. (Araliaceae), *Castanea pumila* (L.) Mill. (Fagaceae), *Helenium amarum* (Raf.) H. Rock (Compositae), *Helianthella* Torr. & A. Gray (Compositae), *Helianthus* L. (Compositae), *Ligustrum* L. (Oleaceae), *Rudbeckia hirta* L. (Compositae), and *Vitex* L. (Lamiaceae) based on labels of examined voucher specimens.

**Discussion.** Detailed morphological and taxonomic remarks about this species are given in Onuferko (2017).

**Material studied. Type material.** Primary: USA: **Illinois:** Carlinville (Macoupin County), C.A. Robertson (*E. lectoides* holotype ♀ [INHS, catalog number: 44383]); **Virginia:** Falls Church, 04.vii.????, N. Banks (*E. semilectus* holotype ♂ [USNM, catalog number: 534053]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAF2273. Specimens examined and sequenced.—Canada: **Ontario:** 2♂ (DEBU).

USA: **Alabama:** Tuskegee National Forest (32.4800° N; 85.6028° W) (Macon County), 24.vii.2016, C.H. Ray (1♀, 1♂, AUMNH); **Nebraska:** 1♂ (BIML); **South Carolina:** 1♀, 2♂ (PCYU).

**Non-barcoded material examined.** Canada: **Ontario:** 15♀, 23♂ (DEBU, PCYU, ROM); Rondeau Provincial Park (42.2814° N; 81.8427° W) (Beach Access #10, near Visitor Centre), 08.viii.2017, R. Ferrari (1♀, 1♂, PCYU).

USA: **Alabama:** Auburn University Ornamental Horticulture Research Center (30.7018° N; 88.1454° W), 09.v.2016, Ray, Clem, and Chowdhury (2♂, AUMNH); Auburn (32.5701° N; 85.4603° W) (Lee County), 20.vi.2015, C.H. Ray (2♂, AUMNH); Autauga County (32.4757° N; 86.8597° W), 12.vi.2016, Ray and Chowdhury (2♂, AUMNH); Autauga County (32.3988° N; 86.7918° W), 12.vi.2016, Ray and Chowdhury (1♂, AUMNH); Grand Bay (30.4763° N; 88.3422° W) (Mobile County), 26.v.2010, S. Martin (1♀, AUMNH); Louise Kreher Forest Ecology Preserve (32.6654° N; 85.4845° W), 02.vii.2016, C.H. Ray (1♀, AUMNH); Randolph County (33.1164° N; 85.5435° W), 22.v.2016, C.H. Ray (1♀, AUMNH); Tuskegee National Forest (32.4788° N; 85.5639° W) (Macon County), 28.v.2016, C.H. Ray (2♀, 2♂, AUMNH); Tuskegee National Forest (32.4816° N; 85.6129° W) (Macon County), 13.viii.2016, C.H. Ray (1♀, AUMNH); Tuskegee National Forest (32.4701° N; 85.5840° W) (Macon County), 24.vii.2016, C.H. Ray (1♀, AUMNH); Tuskegee National Forest (32.4800° N; 85.6028° W) (Macon County), 24.vii.2016, C.H. Ray (1♀, 3♂, AUMNH); **Florida:** Greensboro (Gadsden County), 05.vi.2006, S. Lenberger (1♂, FSCA); Liberty County, 06.vi.2006, S. Lenberger (1♂, FSCA); Shalimar (Okaloosa County), 14.vi.2015, F.W. Eliand, II (1♀, AUMNH); Suwannee River State Park, 24.vi.-14.vii.1977, J.R. Wiley (1♂, FSCA); Torreya State Park (Liberty County), 16.v.1964, H.V. Weems, Jr. (1♀, FSCA); **Kansas:** 2♂ (USNM); **Maryland:** 1♀, 1♂ (BIML, DEBU); **Michigan:** Rose Lake State Wildlife Research Area (42.8075° N; 84.3630° W)

(Shiawassee County), 04.vii.2014, J. Gibbs (1♂, JBWM), 13.vii.2014, J. Gibbs (1♂, JBWM); Warren Dunes State Park (41.9030° N; 86.6040° W) (Berrien County), 06.vii.2014, J. Gibbs (1♀, JBWM); **New Jersey:** 1♀ (BIML); **New York:** 1♀, 2♂ (AMNH); **North Carolina:** 2♀ (AMNH); **North Dakota:** 1♀ (AMNH); 11 mi W Walcott (Richland County), 12.vii.1990, J.R. Powers (1♀, EMEC); 7 mi SE Sheldon (Ransom County), 02.vii.1988, J.R. Powers (1♀, EMEC); **South Carolina:** 1♀ (BIML); **Virginia:** 1♀, 2♂ (BIML).

**31. *Epeolus lectus* Cresson, 1878**

Figs 65, 66, 91B, 92A, & 93A

*Epeolus lectus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 88 (♀).
*Epeolus agnatus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 89 (♂).

**Diagnosis.** The following morphological features in combination can be used to tell *E. lectus* apart from all other North American *Epeolus*: the mesopleuron has sparser punctures ventrolaterally (most i>1d) than in upper half, with the interspaces shining; the metasomal terga have coarse, deep punctures; and T2–T4 have complete and evenly broad fasciae. *Epeolus lectus* is most similar to *E. lectoides*, and in both species the free portion of the axilla is distinctly hooked and the pseudopygidial area of the female is distinctly campanulate with the apex <2 × the medial length, but in *E. lectoides* the metasomal terga have minute, shallow punctures and the T2–T4 fasciae are conspicuously narrowed or interrupted medially.

**Redescription.** FEMALE: Length 9.2 mm; head length 2.3 mm; head width 3.1 mm; fore wing length 7.2 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, tegula, axilla, mesoscutellum, legs, and metasomal sterna. Mandible with apex darker than all but extreme base; preapical tooth lighter than mandibular apex (difficult to see in the *E. lectus* holotype; described from non-type specimens). Flagellum brown and (except F1) slightly lighter than partially dark brown (otherwise orange) scape and F1 and entirely dark brown pedicel, primarily due to extensive pilosity on flagellum. F2 with orange spot basally. Wing membrane dusky subhyaline, slightly darker at apex. Legs from trochanter to

tarsus extensively reddish orange, coxae brown.

*Pubescence.* Face with tomentum densest around antennal socket. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron with upper half sparsely hairy, ventrolateral half nearly bare. Metanotum with tomentum sparser medially, uniformly off white. T1 with discal patch elliptical and very wide, the basal and apical fasciae only narrowly joined laterally. T1 with basal and apical fasciae and T2–T3 with apical fasciae complete (T4 entirely retracted in the *E. lectus* holotype, but with complete fascia in non-type specimens), T2 with fascia with faint anterolateral extensions of sparser tomentum. T5 with two large patches of pale tomentum lateral to and contacting pseudopygidial area at apex. T5 with pseudopygidial area campanulate, its apex less than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 1/3 MOD.

*Surface sculpture.* Punctures dense, but those of head and mesosoma sparser in some areas, larger, deep, and distinct. Labrum with larger punctures than clypeus, but punctures of both equally dense (i<1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla very coarsely and densely punctate; the interspaces shining. Tegula very densely punctate mesally (i≤1d), less so laterally (i=1–2d). Upper half of mesopleuron and anterior margin with denser (i≤1d) punctures than rest of mesopleuron (i>1d), the interspaces shining. Metasomal terga with punctures coarse, dense (i≈1d), evenly distributed on disc; the interspaces shining somewhat.

*Structure.* Preapical tooth blunt and obtuse. Labrum with pair of small subapical denticles, each preceded by small discrete longitudinal ridge. Frontal keel not strongly raised. Scape with greatest length 1.7 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.5). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal (difficult to see in the *E. lectus* holotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla large, its lateral margin (L) half as long as mesoscutellar width (W) (L/W ratio = 0.5) and tip not extending much beyond midlength of mesoscutellum (extending to <2/3 its length in the *E. lectus* holotype and all examined non-type specimens; extending to ~2/3 its length in the *E. agnatus* holotype); axilla with tip

conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion approximately half its medial length; axilla with lateral margin relatively straight and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.2); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered medially and sparser laterally, with the interspaces shining.

**Distribution:** Great Plains and Mountain states east of the Continental Divide (Fig. 66).

**Ecology.** HOST RECORDS: In late July 2015, I collected several specimens of this species near the Poudre River in the Roosevelt National Forest, Colorado, USA, where large numbers of *Colletes* females were collected and observed foraging on purple *Dalea* flowers. Using Stephen's (1954) key, collected specimens were identified as being either *C. robertsonii* Dalla Torre or *C. timberlakei* Stephen, the females of which cannot be reliably distinguished morphologically, although the short triangular mesosomal spines and fine punctation on the tegulae of examined specimens coupled with their collection locality suggest they are *C. timberlakei*.

FLORAL RECORDS: The label of one examined voucher specimen indicates a floral association with *Cryptantha cinerea* var. *jamesii* (Torr.) Cronquist (Boraginaceae).

**Discussion.** The names *Epeolus agnatus* and *E. lectus* were published simultaneously, although Cresson (1878) remarked that *E. agnatus* may be the male of *E. lectus* as the two specimens are structurally similar. Robertson (1902) synonymized *E. agnatus* under *E. lectus*, and separated both specimens from *E. lectoides* based on differences in metasomal pubescence and punctation (see diagnosis). I have examined the holotype specimens of *E. lectus* and *E. agnatus*, and agree with Robertson's treatment. Although Robertson (1902) did not provide any justification for selecting the name *E. lectus* over *E. agnatus*, the holotype of the former is in better condition (that of *E. agnatus* is missing an antenna) and is female, the sex upon which most *Epeolus* species descriptions have been based. While Cresson's *Epeolus* types include remarkably little collection data, the type locality of *E. agnatus* (Dakota Territory) is even more vague than that of *E. lectus* (Kansas).

In contrast to the similar and presumably closely related *E. lectoides*, *E. lectus* has a much more restricted range and is rare in collections. Both species are known from the Great Plains, although the range of *E. lectus* extends further west. In *E. lectus*, the metasoma has much coarser punctures than that of any other North American species in the genus, including *E. lectoides*, in which the metasoma has much finer and sparser punctures. In addition to this and other clear morphological differences (see diagnosis), the distinction between *E. lectus* and *E. lectoides* is supported by separate BINs for the two species.

**Material studied. Type material.** Primary: USA: **Dakota:** H. Ulke (*E. agnatus* holotype ♂ [ANSP, catalog number: 2226]); **Kansas:** Wilson (*E. lectus* holotype ♀ [ANSP, catalog number: 2225]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACZ8246. Specimens examined and sequenced.—USA: **Colorado:** Bellvue (40.6882° N; 105.3070° W) (N Cache La Poudre River and E Gordon Creek, Larimer County), 28.vii.2015, A.T. and T.M. Onuferko (2♀, PCYU).

**Non-barcoded material examined.** USA: **Colorado:** Bellvue (40.6882° N; 105.3070° W) (N Cache La Poudre River and E Gordon Creek, Larimer County), 28.vii.2015, A.T. and T.M. Onuferko (3♀, PCYU); **Kansas:** 4 mi NW Coldwater (Comanche County), 12.vi.2002, G.A. Salsbury (1♀, KUNHM); **South Dakota:** Chamberlain (Brule County), 15.vi.1928, H.C. Severin (1♂, USNM).

**32. *Epeolus mesillae* (Cockerell, 1895)**

Figs 67, 68, & 91D

*Phileremus mesillae* Cockerell, 1895. Psyche (suppl.) 7: 10 (♂), **new neotype designation.**
*Epeolus mesillae* Cockerell, 1934. Am. Mus. Novit. 697: 12.
*Epeolus mesillae palmarum* Linsley, 1939. Pan-Pac. Entomol. 15: 2 (♀), **syn. n.**

**Diagnosis.** The following morphological features in combination can be used to tell *E. mesillae* apart from all other North American *Epeolus*: the axilla does not attain the midlength of the mesoscutellum and like the mesoscutellum is black, the fore wing has two submarginal cells, and T1–T4 have complete fasciae. Only in *E. americanus* and *E. asperatus* is the fore wing commonly with two submarginal cells, but in both species at least the T1 and T2 apical fasciae are interrupted or at least greatly narrowed medially. *Epeolus brumleyi* is similar to *E. mesillae* in axillar structure; in that in females F2 is shorter, as long as wide; and in that T1–T4 have complete fasciae. However, in *E. brumleyi* the axilla is commonly ferruginous in part and the fore wing has three submarginal cells.

**Redescription.** MALE: Length 6.6 mm; head length 1.7 mm; head width 2.4 mm; fore wing length 4.9 mm.

*Integument coloration*. Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, and legs. Mandible orange between dark brown base and reddish-brown apex; preapical tooth slightly lighter than mandibular apex (difficult to see in the *P. mesillae* neotype because mandible closed; described from non-type specimens). Flagellum brown, except F1 extensively orange, and slightly lighter than dark brown scape and pedicel. Pronotal lobe reddish brown. Tegula pale ferruginous to amber. Wing membrane hyaline throughout. Legs, except tarsi, with brown or black more extensive than reddish orange.

*Pubescence.* Face with tomentum densest on clypeus and around antennal socket, sparser on upper paraocular area and vertexal area. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band partly obscured by surrounding pale tomentum. Mesopleuron almost entirely obscured by white tomentum, except where rubbed off in the *P. mesillae* neotype. Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch elliptical, narrow, and short. T2–T6 each with complete fascia, those of T2 and T3 somewhat broader laterally, T2 with fascia with anterolateral extensions of sparser tomentum. S3–S5 with long coppery to silvery subapical hairs.

*Surface sculpture*. Punctures dense. Labrum and clypeus with punctures equally dense (i<1d). Small impunctate spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla

coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i<1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure*. Labrum with pair of small subapical denticles, each preceded by small discrete longitudinal ridge. Frontal keel not strongly raised. Scape with greatest length 1.7 × greatest width. F2 nearly as long as wide (L/W ratio = 0.9). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5–2 MOD at its terminal (difficult to see in the *P. mesillae* neotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin (L) less than half as long as mesoscutellar width (W) (L/W ratio = 0.3) and tip not extending beyond midlength of mesoscutellum; axilla with tip visible, but unattached to mesoscutellum for less than 1/3 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore wing with two submarginal cells. Pygidial plate apically rounded, with large deep punctures closely clustered.

FEMALE: Description as for male except for usual secondary sexual characters and as follows: F2 slightly longer, as long as wide (L/W ratio = 1.0); wing membrane subhyaline, apically dusky; T5 with large, continuous patch of pale tomentum bordering and separate from pseudopygidial area present only in female; T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum; S3–S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~2/5 MOD); pygidial plate apically truncate, with small, denser punctures.

**Distribution:** Known to occur in all major North American deserts (Fig. 68).

**Ecology.** HOST RECORDS: *Colletes clypeonitens* Swenk is the presumed host of *E. mesillae* (Hurd and Linsley 1975). Personal observations support such an association. In Whitewater, California, USA, I have collected large numbers of female *E. mesillae* and male *C. clypeonitens* in an area dominated by creosote bush (*Larrea tridentata* (Sessé & Moc. ex DC.) Coville (Zygophyllaceae)) in late March 2016. Only one specimen (a female) of a different species of *Colletes* (*C. larreae* Timberlake) was taken at the same locality.

FLORAL RECORDS: Collection records from data contributors to Discover Life (Ascher and Pickering 2017) compiled by J. Pickering indicate the following floral associations: *Cryptantha flavoculata* (A. Nelson) Payson, *Erigeron canus* A. Gray, *Heterotheca villosa*, *Larrea tridentata*, and *Potentilla hippiana* Lehm. (Rosaceae). Labels of examined voucher specimens further indicate associations with *Baileya pleniradiata* Harv. & A. Gray ex A. Gray (Compositae), *Chaenactis stevioides* Hook. & Arn. (Compositae), *Dimorphocarpa wislizeni* (Engelm.) Rollins (Brassicaceae), *L. glutinosa* Engelm., *Melilotus* Mill., *Psoralea lanceolata* Pursh (Leguminosae), *Prosopis velutina* Wooton (Leguminosae), and *Tamarix gallica* L. (Tamaricaceae).

**Discussion.** *Epeolus mesillae* was originally described under the now defunct genus *Phileremus* because the fore wing in this species has two rather than three submarginal cells, the typical state for most *Epeolus* species. Among North American *Epeolus*, *E. mesillae* exhibits unusual sexual dimorphism in that in females the fore wing and (to a lesser extent) hind wing are apically dusky whereas in males the wings are hyaline throughout. There is some variability in the pubescence on the metasomal terga among specimens, with some exhibiting more grayish-white than yellowish fasciae. Linsley (1939) recognized specimens from southern California as a distinct subspecies (*E. mesillae palmarum*) based on a larger body size and the presence of pale tomentum interspersed with darker tomentum on the discs of the metasomal terga, especially laterally. Specimens from across the range of this species exhibiting these features have been examined, as well as specimens from southern California in which the metasomal fasciae are clearly distinct from the all-dark discs. Specimens from near the type locality of *E. mesillae palmarum* were barcoded, and their sequences cluster closely with those from specimens from Southeast Arizona and adjacent Sonora, nearer the type locality (Las Cruces, New Mexico) of *E. mesillae mesillae*. Hence, I do not consider these to be distinct subspecies, and herein synonymize *E. mesillae palmarum* under *E. mesillae*, a change in taxonomic status first proposed by Brumley (1965).

I have not seen the male holotype of *P. mesillae* and do not know where it is housed, despite personally searching through the entomological collections where T.D. Cockerell deposited the types of other *Epeolus* species he described. In Brumley (1965), no reference was made to Cockerell's holotype of *P. mesillae*, suggesting Brumley too was unable to find it.

Moreover, no references in the literature to Cockerell's type since the species' original description could be found. In the same publication, another species was described under *Phileremus – P. verbesinae* (now *Neolarra verbesinae* (Cockerell)) –, which was redescribed by Michener (1939) who indicated that the type was in the T.D.A. Cockerell Collection. It is unclear if either specimen has since ended up in an institution that maintains a research collection, but that the holotype of *E. mesillae* has not been referenced since its original description strongly suggests it is unlikely to turn up in the future and to all intents and purposes has been lost. In my search for the holotype at the CUM, a male specimen of *E. mesillae* (labelled as *Phileremus mesillae* Ckll.) from Mesilla Park (the original type locality) collected by Cockerell from *Dimorphocarpa wislizeni* on May 7th was discovered. The specimen, which is the property of the CUM, agrees with the original description, and was used to write the present redescription and diagnosis. Given that a synonymy under *E. mesillae* is proposed herein, it is sensible to have a neotype to serve as a point of reference for any future comparisons. Aside from the collection date, the specimen selected as the neotype of *Phileremus mesillae* fits the description of the original, which can no longer be traced. Hence, in this particular case the qualifying conditions for designating a neotype as listed under Article 75.3 of the International Commission on Zoological Nomenclature (ICZN) Code (http://iczn.org/iczn/index.jsp) seem to have been met.

**Material studied. Type material.** Primary: USA: **California:** Edom (Riverside County), 28.iii.1936, E.G. Linsley (*E. mesillae palmarum* holotype ♀ [CAS, catalog number: 04789]); **New Mexico:** Mesilla Park, 07.v.????, T.D. Cockerell (*P. mesillae* neotype ♂, CUM).

Secondary: USA: **California:** 1 mi W Edom (Riverside County), 28.iii.1936, E.G. Linsley (*E. mesillae palmarum* allotype ♂ [CAS, catalog number: 04790]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAF0161. Specimens examined and sequenced.—Mexico: **Sonora:** 30 km E Agua Prieta (31.3333° N; 109.2403° W), 25.iv.2006, R.L. Minckley (3♀, 1♂, PCYU), 03.v.2005, R.L. Minckley (2♂, PCYU).

USA: **Arizona:** Douglas R/C Flying Field (31.3430° N; 109.4980° W) (Cochise County), 28.iv.2016, T.M. Onuferko (1♀, PCYU); **California:** 31 km N Lucerne Valley (34.6840° N; 116.9605° W) (San Bernardino County), 27.iv.2013, Z.M. Portman (1♂, BBSL); Kelso Dunes

(34.8940° N; 115.7020° W) (Baker, San Bernardino County), 30.iv.2013, A. Ruttan (1♂, PCYU); Tipton Road (33.9079° N; 116.6510° W) (~1.4 mi SW Whitewater, Riverside County), 26.iii.2016, T.M. Onuferko (1♀, PCYU).

**Non-barcoded material examined.** Mexico: **Baja California:** Near La Zapopita Valle de Trinidad, 09-14.iv.1961, F.S. Truxal (2♂, LACM); **Baja California Sur:** 19 mi SW S. Miguel Comondu, 23.vi.1967, E.L. Sleeper and E.M. Fisher (1♂, LACM); **Sonora:** 30 km E Agua Prieta (31.3333° N; 109.2403° W), 03.v.2005, R.L. Minckley (1♀, 5♂, PCYU).

USA: **Arizona:** 11 mi NW Wickenberg, 18.iv.1993, J.G. Rozen (2♀, AMNH); 2 Km W Pima (32.9833° N; 110.2833° W) (Graham County), 25.iv.1996, R.L. Minckley (2♂, PCYU); 2 mi S Willcox (Cochise County), 07.v.1956, E. Ordway (1♀, AMNH); 2.5 mi S Willcox (Cochise County), 24.v.1956, E. Ordway (1♂, AMNH), 07.vi.1956, E. Ordway (1♂, AMNH); 4 mi E Willcox (Cochise County), 08.v.1986, J.G. Rozen (3♀, AMNH), 15.v.1986, J.G. Rozen (1♀, AMNH), 16.v.1986, J.G. Rozen (1♀, AMNH), 17.v.1986, J.G. Rozen (2♀, AMNH); 5 mi NE Douglas (Cochise County), 13.v.1987, J.G. Rozen (1♀, AMNH); Douglas R/C Flying Field (31.3430° N; 109.4980° W) (Cochise County), 23.iv.2016, T.M. Onuferko (2♀, PCYU), 28.iv.2016, T.M. Onuferko (1♀, PCYU); Beaver Dam (36.9028° N; 113.9145° W) (1.7 mi ENE Beaver Dam Wash, Mohave County), 10.v.2014, M.C. Orr (1♀, 1♂, BBSL); Skeleton Canyon Road (Cochise County), 12.v.1977, J.G. Rozen (1♂, AMNH); Southwestern Research Station (5 mi W Portal), 23.iv.1956, E. Ordway (1♀, AMNH); Willcox (Cochise County), 16.v.1985, J.G. Rozen (1♂, AMNH); **California:** 1 mi W Searchlight Junction (San Bernardino County), 21.iii.1971, R.F. Denno and R.W. Rust (1♂, UCBME); 18 mi W Blythe (Riverside County), 22.iv.1978, R.M. Bohart (1♂, UCBME); 25 mi E Twentynine Palms (34.0806° N; 115.5667° W) (Riverside County), 16.iv.2005, L. Packer (1♂, PCYU); 31 km N Lucerne Valley (34.6840° N; 116.9605° W) (San Bernardino County), 27.iv.2013, Z.M. Portman (1♂, BBSL); Borrego Springs (San Diego County), 31.iii.1973, C. Goodpasture (3♂, UCBME); Borrego Valley (San Diego County), 02.iv.1973, R.M. Bohart (1♂, UCBME); Darwin Falls (Inyo County), 12.v.1974, R.M. Bohart (1♀, UCBME); Goffs (San Bernardino County), 24.iv.1993, J.G. and B.L. Rozen (3♀, AMNH), 06.v.1993, J.G. and B.L. Rozen (1♀, AMNH); Morongo Valley (San Bernardino County), 27.iv.1962, O.C. La France (2♂, AMNH); Thousand Palms (Riverside County), 02.iv.1966, R.O. Schuster (1♂, UCBME); Tipton Road (33.9079° N; 116.6510° W) (~1.4 mi SW

Whitewater, Riverside County), 26.iii.2016, T.M. Onuferko (6♀, PCYU); **Colorado:** Foster Ranch (El Paso County), 21.vi.1978, F.M. Brown (1♂, CUM); **Nevada:** 1 mi N Crystal (Nye County), 25.v.1999, L. Packer (1♀, PCYU); 2.8 mi E Wadsworth (Washoe County), 30.vi.1963, G.I. Stage (1♀, AMNH); E Las Vegas (36.0983° N; 115.0025° W) (Clark County), 29.iv.2001, A.L. Hicks and V. Scott (1♀, CUM); Overton (Clark County), 09.v.1958, R.C. Bechtel (1♀, AMNH); Sams Camp Wash (Lincoln County), 10.v.-11.vi.1984, R.C. Bechtel and J.B. Knight (1♀, BBSL); **New Mexico:** 10 mi S Animas (Hidalgo County), 15.v.2013, J.G. Rozen (1♂, AMNH); 15 mi E Animas (Hidalgo County), 15.v.2013, J.G. Rozen (3♂, AMNH); Carlsbad (Eddy County), 20.v.1969, Brothers, Krueger, and Michener (1♂, KUNHM); Road Forks (Hidalgo County), 16.v.2013, J.G. Rozen (2♂, AMNH); **Texas:** 20 km S Kent (Jeff Davis County), 30.iv.2003, L. Packer and G. Fraser (1♀, PCYU); 7.6 mi S Van Horn (Culberson County), 27.iv.1979, R.R. Snelling (1♂, LACM); Chihuahuan Desert Research Institute (Jeff Davis County), 29.iv.2003, L. Packer and G. Fraser (2♀, PCYU); **Utah:** Dry Fork (Kane County), 22.v.2000, O. Messinger (1♀, BBSL).

**33. *Epeolus minimus* (Robertson, 1902)**

Figs 69, 70, & 101

*Triepeolus minimus* Robertson, 1902. Entomol. News 13: 81 (♀).
*Argyroselenis minima* Robertson, 1903. Can. Entomol. 35: 284.
*Epeolus beulahensis* Cockerell, 1904. Ann. Mag. Nat. Hist. 13: 40 (♀).
*Epeolus lutzi* Cockerell, 1921. Am. Mus. Novit. 23: 16 (♂).
*Epeolus lutzi dimissus* Cockerell, 1921. Am. Mus. Novit. 23: 16 (♀).
*Epeolus arciferus* Cockerell (in Cockerell and Sandhouse, 1924). Proc. Calif. Acad. Sci. (4) 13: 319 (♀).
*Epeolus pilatei* Cockerell (in Cockerell and Sandhouse, 1924). Proc. Calif. Acad. Sci. (4) 13: 320 (♀).
*Epeolus eastwoodae* Cockerell, 1937. Pan-Pac. Entomol. 13: 149 (♂).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. minimus* apart from all

other North American *Epeolus* except *E. banksi* and *E. olympiellus*: in females, F2 is at least 1.2 × as long as wide; the mesoscutum has distinct, evenly broad paramedian bands that may be joined posteriorly; the axilla is small to intermediate in size, not extending much beyond the midlength of the mesoscutellum (extending to <2/3 its length) but the free portion is more than 1/4 as long as the entire medial length of the axilla, and the axilla (except sometimes the tip) and mesoscutellum are black; the mesopleuron is closely (most i<1d) and evenly punctate; T1 has a quadrangular discal patch, in dorsal view the longitudinal band is at least half as wide as the breadth of the apical fascia; and the T2 fascia has lobe-like anterolateral extensions of tomentum. Whereas in *E. banksi* the mesoscutum and metasomal terga have bands of gray short appressed setae, in *E. minimus* the mesoscutum and metasomal terga have bands of off-white to pale yellow short appressed setae. In this respect, *E. minimus* more closely resembles *E. olympiellus*, but in *E. olympiellus* the T3 and T4 fasciae are broken or at least narrowed laterally, as well as medially, whereas in *E. minimus* the T3 and T4 fasciae are not broken laterally, and are complete or narrowly interrupted medially. *Epeolus minimus* is also similar to *E. axillaris*, but in *E. axillaris* the metanotum has a distinct posteromedial depression (as opposed to being flat) and the axilla is more elongate, extending well beyond the midlength of the mesoscutellum but not as far back as its posterior margin.

**Redescription.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Widely distributed across Canada and the United States, although apparently more common in the west; not known to occur in parts of northeastern North America or the high arctic (Fig. 70). Also, the single (perhaps mislabelled) examined specimen from Florida is an extreme outlier, and given the lack of other examined material from the Southern United States the record should be treated with some skepticism.

**Ecology.** HOST RECORDS: Graenicher (1906) associated *E. minimus* (as *A. minima*) with *C. eulophi* Robertson based on detailed observations of a female of the former inspecting and entering the nest of a female of the latter in Lake Woods, Wisconsin, USA. However, according to Stephen (1954) Graenicher's record of *C. eulophi* in Wisconsin is based on observations of *C. kincaidii*. *Epeolus minimus* has been collected with *C. kincaidii* in Birds Hill Provincial Park and

Spruce Woods Provincial Park, Manitoba, Canada where no *C. eulophi* were collected or observed (J. Gibbs, personal communication, 2017), so the association between *E. minimus* and *C. kincaidii* seems likely.

FLORAL RECORDS: See Onuferko (2017). Floral associations are also indicated in Suppl. material 1, which includes newly discovered associations with *Ericameria nauseosa* var. *nauseosa* and *Medicago* L. (Leguminosae) based on labels of examined voucher specimens.

**Discussion.** In Onuferko (2017), *E. minimus* is said to be similar to a Californian species yet to be formally recognized, which herein is formally described under the name *Epeolus axillaris*. Detailed morphological and taxonomic remarks about this species are given in Onuferko (2017). *Epeolus minimus* is among the most widespread and commonly collected *Epeolus* species in North America.

**Material studied. Type material.** Primary: USA: **California:** Cuyler's Cove (San Miguel Island), 27.vii.1937, T.D. Cockerell (*E. eastwoodae* holotype ♂ [CAS, catalog number: 04651]); Pacific Grove (Monterey County), ix.1920, F.E. Blaisdell (*E. arciferus* holotype ♀ [CAS, catalog number: 01614]); San Pedro, 25.x.1909, G.R. Pilate (*E. pilatei* holotype ♀ [CAS, catalog number: 01615]); **Colorado:** Leadville, 03-05.viii.1919 (*E. lutzi dimissus* holotype ♀ [AMNH, catalog number: 25099]); Walsenburg, 14.vi.1919 (*E. lutzi* holotype ♂ [AMNH, catalog number: 25098]); **Illinois:** Carlinville (Macoupin County), C.A. Robertson (*T. minimus* holotype ♀ [INHS, catalog number: 62276]); **New Mexico:** Beulah, 11.vii.????, T.D. Cockerell (*E. beulahensis* holotype ♀ [USNM, catalog number: 534040]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAD3554. Specimens examined and sequenced.—Canada: **Alberta:** 2♂ (PCYU); **British Columbia:** Haynes' Lease Ecological Reserve (49.0930° N; 119.5200° W), 29.vi.-01.vii.2011, G.A. Gielens (1♀, RSKM); **Manitoba:** Spruce Woods Provincial Park (49.6630° N; 99.2790° W) (Spirit Sands, Division 7), 07.vii.2017, J. Gibbs and Nozoe (1♀, 1♂, JBWM); **Ontario:** 1♀, 1♂ (PCYU); **Saskatchewan:** 3♂ (PCYU); Saskatchewan Landing Provincial Park (50.6950° N; 107.9030° W), 03.vii.2013, A. Fortney and M. Anderson (1♂, RSKM); **Yukon:** 1♂ (RSKM).

USA: **California:** 1♂ (EMEC); **Colorado:** 2♀ (PCYU); Morrison (39.6677° N; 105.1968° W) (SE Red Rocks Amphitheatre), 16.vi.2017, T.M. Onuferko (1♂, PCYU); **Idaho:** 2♀, 1♂ (BBSL, PCYU); **Utah:** 1♀ (BBSL).

**Non-barcoded material examined.** Mexico: **Baja California:** San Vicente, 08.vii.1963, J. Powell (3♂, EMEC).

Canada: **Alberta:** 15♀, 10♂ (CNC); **British Columbia:** 16♀, 1♂ (CNC, ROM); **Manitoba:** 4♀, 7♂ (CNC, DEBU, ROM); Birds Hill Provincial Park (50.0100° N; 96.9100° W) (Division 12), 15.vii.2017, J. Gibbs and Nozoe (1♂, JBWM); Erickson, 03.viii.1983, D.H. Pengelly (1♀, JBWM); Fort Whyte (Winnipeg), 20.vi.1991, B.G. Elliot (1♂, JBWM), 13.vii.1991, B.G. Elliot (1♂, JBWM); Portage la Prairie, 29.vi.1976, T.D. Galloway (1♀, JBWM); Spruce Woods Provincial Park (49.6630° N; 99.2790° W) (Spirit Sands, Division 7), 07.vii.2017, J. Gibbs and Nozoe (1♂, JBWM); Winnipeg, 21.vi.1979, T.D. Galloway (1♂, JBWM), 06.vii.1991, B.G. Elliot (1♂, JBWM); Winnipeg Beach, 15.vii.1989, T.D. Galloway (1♀, JBWM), 15.vii.1989, T.D. Galloway (2♂, JBWM); **Northwest Territories:** 7♀ (CNC); **Ontario:** 9♀, 6♂ (CNC, PCYU, ROM); Caledon (Forks of the Credit Provincial Park), 25.vii.1968, P. MacKay (1♂, PCYU); **Quebec:** 3♂ (CNC); **Saskatchewan:** 9♀, 10♂ (CNC, PCYU); Borden Bridge, 01.viii.1976, T.D. Galloway (1♀, JBWM); Ernfold, 05.vii.1984, T.D. Galloway (1♀, JBWM); Sands Hills (7 km W Piapot), 26.vii.2003, D. Larson (1♂, PCYU); **Yukon:** 2♀ (CNC).

USA: **California:** 4♀, 4♂ (EMEC, UCR); 2 mi S Asilomar (Monterey County), 26.ix.1959, C.W. O'Brien (1♂, AMNH); Antioch (Contra Costa County), 20.ix.1958, J.R. Powers (1♀, AMNH), 28.viii.1976, N.J. Smith (1♀, UCBME); Bodega Head (Sonoma County), 14.v.1977, W.M. Oldham (1♂, UCBME); Carnelian Bay (Lake Tahoe), 29.vii.1962, R.M. Bohart (1♀, UCBME); Carson Pass (Alpine County), 13.vii.1966, R.M. Bohart (1♂, UCBME), 16.vii.1968, R.M. Bohart (1♂, UCBME), 16.vii.1968, W.W. Harberts (1♂, UCBME); Chipmunk Flat (Tuolumne County), 09.viii.1960, C.A. Toschi (1♀, AMNH); Dune Lakes (3 mi S Oceano, San Luis Obispo County), 01.vi.1972, J. Powell (1♂, EMEC), 03-04.x.1972, J. Powell (18♂, EMEC), 07.vi.1973, J. Powell (1♂, EMEC), 11.vii.1973, R. Coville (1♂, EMEC), 12.vii.1973, J. Powell (2♂, EMEC), 02.v.1974, J. Powell (1♂, EMEC); Holcomb Valley (San Bernardino County) (1♂, BBSL); Hot Creek (8 air mi E Mammoth Lakes, Mono County), 24.viii.1977, J.

Powell (2♂, EMEC); Inglenook Fen (5 mi N Fort Bragg, Mendocino County), 27.v.1976, R. Coville (1♀, 3♂, EMEC); Inglenook Fen (Mendocino County), 22.vii.1972, E.I. Schlinger (1♂, EMEC); Lanphere-Christensen Dunes Preserve (4 mi W Arcata, Humboldt County), 26.vii.1975, M.E. Buegler and E.I. Schlinger (1♂, EMEC); Lobos Creek (San Francisco County), 10.v.1979, J. Powell (1♀, 3♂, EMEC), 15.vi.1960, G.I. Stage (1♀, AMNH); Mad River Beach (Humboldt County), 26.vi.1969, J. Powell (1♀, EMEC); McClures Beach (Marin County), 27.vi.1969, R.W. Thorp (1♀, UCBME); North Beach (Point Reyes National Seashore, Marin County), 10.v.1980, K. Standow (1♀, EMEC), 30.viii.1974, P.A. Opler (2♀, 1♂, EMEC); North Fork, Del Puerto Creek (Del Puerto Canyon, Stanislaus County), 25.v.1974, E. Schlinger (1♂, EMEC); Point Reyes National Seashore (Marin County), 03.iii.1968, R.W. Thorp (1♀, UCBME), 23.vii.1974, P.A. Opler (1♀, EMEC); San Bruno Mountain (San Mateo County), 23.v.1961, G.I. Stage (1♀, AMNH), 23.v.1961 (1♀, AMNH), 23.viii.1960, G.I. Stage (1♂, AMNH); San Francisco Bay Salt Marshes, viii.1907?, Thompson (3♂, EMEC); San Francisco Sand Dunes, 25.vi.1954, J.G. Rozen (1♂, EMEC), 25.vi.1954, P.D. Hurd (1♀, EMEC); Santa Cruz Island (Christi Beach, Santa Barbara County), 23.ix.1968, R.W. Thorp (1♀, UCBME); Sierra Valley (Sierra County), 06.vii.1972, R.M. Bohart (1♀, UCBME); Simonton Cove (San Miguel Island, Santa Barbara County), 11.vii.1970, A.A. Grigarick and R.C. Schuster (1♀, UCBME); Toms Place (Mono County), 01.ix.1965, A.J. Slater (1♀, EMEC); Yuba Pass (Sierra County), 11.viii.1978, R.M. Bohart (1♂, KUNHM); **Colorado:** Rock Creek Park (Colorado Springs), 19.viii.1937 (1♀, 1♂, AMNH); **Florida:** 1♀ (PCYU); **Idaho:** 1♀ (PCYU); Daniels Reservoir (Oneida County), 11.vii.1997, F.D. Parker (3♂, BBSL); **Illinois:** 1♂ (FMNH); **Minnesota:** Detroit, 26.viii.1924, O.A. Stevens (1♀, AMNH); **Montana:** 1♀ (KUNHM); 11 mi SE Ennis (Madison County), 18.viii.1966, D.R. Miller (1♀, UCBME); **Nebraska:** Cedar Point Biological Station (8 mi N Ogallala, Keith County), 11-18.vii.1988, J.G. Rozen and E. Quinter (1♀, AMNH); Fort Robinson (Dawes County), 11.viii.1971, J.G., B.L., and K.C. Rozen (3♀, AMNH), 12.viii.1971, J.G., B.L., and K.C. Rozen (2♀, AMNH), 09-11.viii.1972, J.G. Rozen, K.C. Rozen, and R. McGinley (2♀, 4♂, AMNH); Warbonnet Canyon (Sioux County), 24.vii.1968, R.R. Snelling (1♂, LACM); **Nevada:** Fallon, 01.vi.1930, E.L. Bell (1♀, AMNH), 06.vi.1930, E.L. Bell (1♀, AMNH), 10.vi.1930, E.L. Bell (1♀, AMNH); Mount Rose Summit (Washoe County), 09.vii.1964, R.M. Bohart (1♀, UCBME); **New Mexico:** Santa Fe, 09.vi.1931, F.E. Lutz (1♀, 1♂, AMNH); **North Dakota:** Gascoyne, 19.vi.1918, O.A. Stevens (1♀, AMNH); Jamestown,

16.viii.1913, O.A. Stevens (1♀, AMNH); Marmarth, 04.vii.1949, O.A. Stevens (3♂, AMNH); McKenzie, 05.viii.1913, O.A. Stevens (1♀, AMNH); Monango, 03.vii.1913, O.A. Stevens (1♀, AMNH); Pleasant Lake, 11.viii.1913, O.A. Stevens (1♀, AMNH); Washburn, 23.vii.1926, O.A. Stevens (3♀, 2♂, AMNH); Williston, 09.viii.1915, O.A. Stevens (1♂, AMNH); **Oregon:** 1♂ (KUNHM); **South Dakota:** 1♀ (BIML); **Utah:** Indian Canyon (Duchesne County), 18.vii.1965, G.F. Knowlton (1♀, UCBME); NE Ruby's Inn (Garfield County), 17.viii.1995, V.J. Tepedino and F.D. Parker (2♀, BBSL).

**34. *Epeolus nebulosus* new species**

Figs 71, 72, & 99A

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. nebulosus* apart from all other North American *Epeolus* except *E. basili*, *E. novomexicanus*, and *E. pusillus*: the axilla is large, with the tip extending well beyond the midlength of the mesoscutellum but at most to the band of pale tomentum along its posterior margin, dilated laterally, and ferruginous to some degree whereas the mesoscutellum is typically all black; the axilla's free portion is clearly less than 2/5 as long as its entire medial length; the mesopleuron is closely (most i<1d) and evenly punctate, that of the female is obscured by white tomentum only in the upper half (with a large, sparsely hairy circle occupying much of the ventrolateral half) whereas that of the male (excluding the hypoepimeral area) is entirely obscured by white tomentum; T2–T4 have complete and evenly broad fasciae; the T2 fascia has lobe-like anterolateral extensions of tomentum; and the pseudopygidial area of the female is lunate and wider than long (the apex ≤2 × the medial length). *Epeolus basili*, *E. nebulosus*, *E. novomexicanus*, and *E. pusillus* are all extremely similar to one another. *Epeolus nebulosus* is most similar to *E. novomexicanus*, but in *E. novomexicanus* the mesoscutum usually has distinct paramedian bands and at least the integument beneath the T1 apical fascia is ferruginous, as are sometimes the rest of the tergum and other terga, whereas in *E. nebulosus* the mesoscutum is entirely obscured by pale tomentum and the metasomal terga (excluding the brown translucent apical margins) are entirely black. In *E. basili* the metasomal terga are also ferruginous to some degree, and the T2 and T3 (for female) or T2–T4 (for male) fasciae are narrowed medially and removed from the apical margin

(in *E. nebulosus* the T2–T4 fasciae are on or very little removed from the apical margin), and the pseudopygidial area of the female is ≥2 × the medial length. Whereas in *E. pusillus* the flagellum, except sometimes F1, and metasomal sterna are consistently brown or black and clearly not the same reddish-orange color as the legs (tibiae to tarsi), in *E. nebulosus* the flagellum, at least ventrally, is the same reddish-orange color as the legs (tibiae to tarsi) as are usually the metasomal sterna. *Epeolus nebulosus* is also similar to *E. scutellaris* in that the axilla is large, with the lateral margin arcuate, and that the apical fasciae are complete. However, in *E. scutellaris* the pseudopygidial area of the female is much wider (the apex ~2.5–3 × the medial length) than in *E. nebulosus*, and the mesopleuron of both the female and male is obscured by white tomentum only in the upper half (with a large, sparsely hairy circle occupying much of the ventrolateral half).

**Description.** MALE: Length 7.2 mm; head length 2.0 mm; head width 2.7 mm; fore wing length 5.5 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, legs, pygidial plate, and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth slightly lighter than mandibular apex. Antenna brown and orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black. S1–S6 reddish orange.

*Pubescence.* Face with tomentum densest on clypeus and around antennal socket, slightly sparser on upper paraocular area and vertexal area. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum largely obscured by pale tomentum. Mesopleuron (excluding hypoepimeral area) entirely obscured by white tomentum. Metanotum with tomentum uninterrupted, uniformly off white. T1 with narrow and short discal patch largely obscured by pale tomentum. T2–T6 each with complete fascia, T2 with fascia with wide basomedially convergent anterolateral extensions of tomentum. S4 and S5 with long coppery to silvery subapical hairs, which individually are often darker apically.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d) (difficult to see in holotype because clypeus entirely obscured by tomentum; described from paratypes with hair removed). Small impunctate shiny spot lateral to lateral

ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally (i≤1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i<1d) to rugose; mesopleuron with punctures more or less equally dense throughout (not visible in holotype because mesopleuron entirely obscured by tomentum; described from paratypes). Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth obtuse. Labrum with pair of small subapical denticles not preceded by carinae (difficult to see in holotype; described from paratypes). Frontal keel not strongly raised. Scape with greatest length 2.0 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.2). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5 MOD at its terminal. Mesoscutellum weakly bigibbous. Axilla large, its lateral margin (L) half as long as mesoscutellar width (W) (L/W ratio = 0.5) and tip extending well beyond midlength of mesoscutellum but not as far back as its posterior margin; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically rounded, with large deep, well-separated punctures, with the interspaces shining.

FEMALE: Description as for male except for usual secondary sexual characters and as follows: F2 even longer than wide (L/W ratio = 1.5); mesopleuron densely hairy, except for two almost entirely bare patches (one beneath base of fore wing (hypoepimeral area), a larger circular patch occupying much of ventrolateral half of mesopleuron); T5 with large, continuous patch of pale tomentum bordering and contacting pseudopygidial area present only in female; T5 with pseudopygidial area lunate, its apex twice as wide as medial length, indicated by silvery setae on disc of apicomedial region elevated from rest of tergum; S4 and S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by much more than 1/4 MOD); pygidial plate apically truncate, with small, denser punctures.

**Etymology.** The name is in reference to the pale tomentum obscuring much of the integument of this species. From the Latin, “nebulosus” (hazy).

**Distribution:** California and probably western Nevada (Fig. 72).

**Ecology.** HOST RECORDS: The host species of *E. nebulosus* is/are presently unknown.

FLORAL RECORDS: Labels of examined voucher specimens indicate a floral association with *Ericameria nauseosa*.

**Discussion.** *Epeolus nebulosus* is a cryptic species within the "*pusillus* group" that closely resembles some specimens of *E. novomexicanus*, and the ranges of the two species overlap to some extent. The morphological differences (in integument coloration and patterns of pubescence) among the four members of the "*pusillus* group" are subtle. The status of *E. nebulosus* as a separate species is further supported by a separate BIN and large barcode sequence divergence (>3.2%) from its nearest neighbor, *E. novomexicanus*. Although most species of *Epeolus* were described from a female name-bearing type, a male specimen is designated as the holotype of *E. nebulosus* because a barcode-compliant sequence is associated with it and because much of the pubescence is discolored or rubbed off in the available female specimen, which is herein designated as the allotype. Since this species is described from very few specimens, efforts should be made to collect additional representatives of *E. nebulosus* for DNA barcoding to determine if the morphological differences between it and *E. novomexicanus* reported here are consistent.

**Material studied. Type material.** Primary: USA: **California:** Gilbert Pass on Hwy 168 (37.4305° N; 117.9388° W) (N Deep Springs Valley, Inyo County), 14.ix.2013, M.C. Orr (holotype ♂ [CCDB-28239 F01], BBSL).

Secondary: USA: **California:** 3.2 km S Pearblossom (Los Angeles County), 07.xi.1977, R.R. Snelling (allotype ♀, LACM); Gilbert Pass on Hwy 168 (37.4305° N; 117.9388° W) (N Deep Springs Valley, Inyo County), 14.ix.2013, M.C. Orr (paratypes 2♂, BBSL).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACZ0767. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**35. *Epeolus novomexicanus* Cockerell, 1912**

Figs 73, 74, 97E, & 99B

*Epeolus novomexicanus* Cockerell, 1912. Ann. Mag. Nat. Hist. (8) 10: 487 (♂).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. novomexicanus* apart from all other North American *Epeolus* except *E. basili*, *E. nebulosus*, and *E. pusillus*: the axilla is large, with the tip extending well beyond the midlength of the mesoscutellum but at most to the band of pale tomentum along its posterior margin, dilated laterally, and ferruginous to some degree whereas the mesoscutellum is typically all black; the axilla's free portion is clearly less than 2/5 as long as its entire medial length; the mesopleuron is closely (most i<1d) and evenly punctate, that of the female is obscured by white tomentum only in the upper half (with a large, sparsely hairy circle occupying much of the ventrolateral half) whereas that of the male (excluding the hypoepimeral area) is entirely obscured by white tomentum; T2–T4 have complete and evenly broad fasciae; the T2 fascia has lobe-like anterolateral extensions of tomentum; and the pseudopygidial area of the female is lunate and wider than long (the apex ≤2 × the medial length). *Epeolus basili*, *E. nebulosus*, *E. novomexicanus*, and *E. pusillus* are all extremely similar to one another. *Epeolus novomexicanus* is most similar to *E. nebulosus*, but in *E. nebulosus* the mesoscutum is entirely obscured by pale tomentum and the metasomal terga (excluding the brown translucent apical margins) are entirely black whereas in *E. novomexicanus* the mesoscutum usually has distinct paramedian bands and at least the integument beneath the T1 apical fascia is ferruginous, as are sometimes the rest of the tergum and other terga. In *E. basili* the metasomal terga are also ferruginous to some degree, but the T2 and T3 (for female) or T2–T4 (for male) fasciae are narrowed medially and removed from the apical margin (in *E. novomexicanus* the T2–T4 fasciae are on or very little removed from the apical margin), and the pseudopygidial area of the female is ≥2 × the medial length. Whereas in *E. pusillus* the flagellum, except sometimes F1, and metasomal sterna are consistently brown or black and clearly not the same reddish-orange color as the legs (tibiae to tarsi), in *E. novomexicanus* the flagellum, at least ventrally, is the same reddish-orange color as the legs (tibiae to tarsi) as are usually the metasomal sterna. *Epeolus novomexicanus* is also similar to *E. scutellaris* in that the axilla is large, with the lateral margin arcuate, and that the apical fasciae are complete. However, in *E. scutellaris* the pseudopygidial area of the female is much wider (the apex ~2.5–3 × the

medial length) than in *E. novomexicanus*, and the mesopleuron of both the female and male is obscured by white tomentum only in the upper half (with a large, sparsely hairy circle occupying much of the ventrolateral half).

**Redescription.** MALE: Length 6.1 mm; head length 1.7 mm; head width 2.3 mm; fore wing length 4.4 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, legs, metasomal terga (including pygidial plate), and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth slightly lighter than mandibular apex (difficult to see in holotype because mandible closed; described from non-type specimens). Antenna brown and orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black. S1–S6 reddish orange.

*Pubescence.* Face with tomentum partly rubbed off in holotype, but white and densest around antennal socket in non-type specimens. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band partly obscured by surrounding pale tomentum. Mesopleuron (excluding hypoepimeral area) entirely obscured by white tomentum (except where rubbed off in holotype). Metanotum with tomentum uninterrupted, uniformly off white. T1 with narrow and short discal patch partly obscured by pale tomentum. T2–T5 each with complete fascia (T6 mostly retracted in holotype, but with complete fascia in non-type specimens), T2 with fascia with wide basomedially convergent anterolateral extensions of tomentum. S4 and S5 with long coppery to silvery subapical hairs, which individually are often darker apically.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate (i≤2d). Mesopleuron with ventrolateral half densely punctate (i<1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth obtuse. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.8 × greatest width. F2 as long as wide (L/W ratio = 1.0). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum weakly bigibbous. Axilla large, its lateral margin (L) half as long as mesoscutellar width (W) (L/W ratio = 0.5) and tip extending well beyond midlength of mesoscutellum but not as far back as its posterior margin; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically rounded, with large deep punctures closely clustered.

FEMALE: Description as for male except for usual secondary sexual characters and as follows: F2 noticeably longer than wide (L/W ratio = 1.5); mesopleuron densely hairy, except for two sparsely hairy circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron); T5 with large, continuous patch of pale tomentum bordering and contacting pseudopygidial area present only in female; T5 with pseudopygidial area lunate, its apex less than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum; S4 and S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~1/3 MOD); pygidial plate apically truncate, with small, denser punctures.

**Distribution:** Western North America (Fig. 74).

**Ecology.** HOST RECORDS: Torchio (1965) reported an association between *E. pusillus* (identified as such by R. Brumley) and *C. ciliatoides* Stephen (identified as such by W. Stephen, who in 1954 described the species) based on observations of females of the former entering the nests of females of the latter from an aggregation near Delta, Utah, USA. Brumley (1965) noted that a series of *E. pusillus* specimens taken from the Great Basin (primarily Utah) differed from other members of that species in having a reddish orange labrum, clypeus, antenna, mesopleuron, and metasomal terga and/or sterna; broader metasomal fasciae; and often denser pubescence on the mesoscutum. Herein, specimens matching that description are recognized as a separate albeit closely-related species, *E. novomexicanus*, which Brumley (1965) considered to be synonymous with *E. crucis*, a name herein synonymized under *E. compactus*.

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Chrysothamnus* (possibly in reference to plants that now are in the genus *Ericameria*), *Erigeron* L., *Haplopappus* Cass. (Compositae), *Helianthus*, *Lupinus* L. (Leguminosae), *Machaeranthera* Nees (Compositae), and *Senecio spartioides* Torr. & A. Gray.

**Discussion.** Brumley (1965) considered *E. novomexicanus* and *E. rufulus* to be synonyms of *E. crucis*, a name which herein is recognized as a synonym of *E. compactus*. Here, *E. novomexicanus* and *E. rufulus* are considered to be valid names associated with two very different species, with the former most closely resembling *E. basili*, *E. nebulosus*, and *E. pusillus*. Although sequenced specimens of *E. novomexicanus* and *E. pusillus* share the same BIN, and were previously all regarded as *E. pusillus* (Onuferko 2017), the difference in coloration and pubescence between the two forms is as pronounced as, if not more than, that between the true *E. pusillus* and sequenced representatives of the two members of the "*pusillus* group" (*E. basili* and *E. nebulosus*) that were assigned separate BINs. Hence, with strong molecular support for partitioning this species group into three distinct clusters in which four distinct forms can be recognized morphologically, I have opted to treat *E. novomexicanus* and *E. pusillus* as heterospecific. The holotypes (both males) of *E. nebulosus* and *E. novomexicanus* are similarly covered in dense tomentum and closely resemble one another, and it should be noted that sequenced specimens resembling the holotypes of both species but from nearer the type locality of *E. novomexicanus* were assigned a BIN that is not shared with *E. nebulosus* but is instead shared with *E. pusillus*.

**Material studied. Type material.** Primary: USA: **New Mexico:** Santa Fe, 02.viii.1912, T.D. Cockerell (holotype ♂ [USNM, catalog number: 534049]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAX7180. Specimens examined and sequenced.—USA: **Utah:** 4.17 mi SE Wig Mountain (40.2876° N; 113.0390° W) (Toole County), 26.ix.2005, T.L. Griswold (1♀, BBSL); Beef Basin Rd (38.0846° N; 109.5765° W) (N Cottonwood Creek, San Juan County), 03.x.2014, M.C. Orr (1♀, BBSL).

**Non-barcoded material examined.** USA: **Arizona:** Near Hyde Park (Coconino County), 28.ix.1964, Timberlake (1♂, USNM); **California:** 8 mi W Coalinga (Fresno County), 28.ix.1957, R.R. Snelling (1♂, LACM); Los Angeles County, ix.????, Coquillett (1♀, USNM); Sugar Loaf Mountain (Modoc County), 12.ix.1969, E.E. Grissell and R.F. Denno (1♀, 1♂, UCBME); Victorville, 28.ix.1938, Timberlake (1♂, USNM); **Colorado:** Boulder (Boulder County), 28.viii.1976, U.N. Lanham (1♂, CUM); Great Sand Dunes National Monument (Alamosa County), 22.ix.1979, F.M. Brown (1♀, CUM); Great Sand Dunes National Monument (37.6629° N; 105.6212° W) (Alamosa County), 24.viii.2000, A.L. Hicks and V. Scott (1♀, 5♂, CUM); White Rocks (Boulder County), 24.vii.1934, C.H. Hicks (1♀, CUM); **Idaho:** Homedale, 16.viii.1974, R.M. Bohart (1♀, 1♂, UCBME); **Montana:** Ashland (Rosebud County), 11.viii.1970, D.R. Miller (1♀, USNM); **Nebraska:** Smiley Canyon (42.7964° N; 103.4045° W) (Fort Robinson State Park, Sioux County), 05.ix.1999, A.L. Hicks and V. Scott (1♀, CUM); **Nevada:** The Needle Rocks (N end Pyramid Lake, Washoe County), 15.ix.1983, J. Doyen (1♂, EMEC); **New Mexico:** Laguna, 07.viii.1966, D.R. Miller (1♀, 1♂, UCBME); Near Tecolote, 05.ix.??30 (1♀, USNM); White Sands National Monument (near Alamogordo), 01.ix.1940, H.G. Rodeck (1♂, CUM); **North Dakota:** 1 mi SE McLeod (Ransom County), 26.viii.1972, J.R. Powers (1♀, EMEC); **Oregon:** Deep Creek (1 mi E Adel, Lake County), 13.ix.1969, R.F. Denno and E.E. Grissell (2♂, UCBME); **Utah:** 0.5 mi S Springdell (Uinta National Forest), 22.viii.1963, C.W. O'Brien (1♂, AMNH); 1 mi N Kitchen Corral Spr 12S (Kane County), 10.ix.2002, L. Topham (1♀, BBSL); 13.2 mi N Blanding (San Juan County), 24.viii.??67, J.C. Hall (1♂, USNM); 16 mi W Tropic (37.3913° N; 112.2575° W) (Garfield County), 28.vii.2008, T.L. Griswold (1♀, BBSL); Beryl (Iron County), 27.ix.1953, M. Cazier (1♀, AMNH).

### 36. *Epeolus olympiellus* Cockerell, 1904

Figs 75 & 76

*Epeolus olympiellus* Cockerell, 1904. Ann. Mag. Nat. Hist. 13: 41 (♂).
*Epeolus tristicolor* Viereck, 1905. Can. Entomol. 37: 280 (♀).
*Epeolus humillimus* Cockerell, 1918. Ann. Mag. Nat. Hist. (9) 1: 160 (♂).
*Epeolus rufomaculatus* Cockerell and Sandhouse, 1924. Proc. Calif. Acad. Sci. (4) 13: 314 (♀).
*Epeolus rubrostictus* Cockerell and Sandhouse, 1924. Proc. Calif. Acad. Sci. (4) 13: 318 (♀).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. olympiellus* apart from all other North American *Epeolus* except *E. banksi* and *E. minimus*: in females, F2 is at least 1.2 × as long as wide; the mesoscutum has distinct, evenly broad paramedian bands that may be joined posteriorly; the axilla is small to intermediate in size, not extending much beyond the midlength of the mesoscutellum (extending to <2/3 its length) but the free portion is more than 1/4 as long as the entire medial length of the axilla, and the axilla (except sometimes the tip) and mesoscutellum are black; the mesopleuron is closely (most i<1d) and evenly punctate; T1 has a quadrangular discal patch, in dorsal view the longitudinal band is at least half as wide as the breadth of the apical fascia; and the T2 fascia has lobe-like anterolateral extensions of tomentum. Whereas in *E. banksi* the mesoscutum and metasomal terga have bands of gray short appressed setae, in *E. olympiellus* the mesoscutum and metasomal terga have bands of off-white to pale yellow short appressed setae. In this respect, *E. olympiellus* more closely resembles *E. minimus*, but in *E. minimus* the T3 and T4 fasciae are not broken laterally, and are complete or narrowly interrupted medially, whereas in *E. olympiellus* the T3 and T4 fasciae are broken or at least narrowed laterally, as well as medially. Whereas throughout most of its range *E. minimus* exhibits reddish-orange coloration on the labrum, antenna, pronotal lobe, and/or legs, except foreleg, from trochanters to tarsi, in *E. olympiellus* the labrum, antenna, and legs from coxae to femora are brown or black. *Epeolus olympiellus* is also similar to *E. axillaris*, but in *E. axillaris* the metanotum has a distinct posteromedial depression (as opposed to being flat) and the axilla is more elongate, extending well beyond the midlength of the mesoscutellum but not as far back as its posterior margin.

**Description.** This species was recently redescribed (Onuferko 2017).

**Distribution:** United States west of the Rocky Mountains to southern British Columbia (Fig. 76).

**Ecology.** See Onuferko (2017) for host and floral records. Floral associations are also indicated in Suppl. material 1.

**Discussion.** Detailed morphological and taxonomic remarks about this species are given in Onuferko (2017).

**Material studied. Type material.** Primary: Canada: **British Columbia:** Nanaimo (Nanaimo Biological Station), 24.vi.1920, E.P. Van Duzee (*E. rubrostictus* holotype ♀ [CAS, catalog number: 01613]); Vancouver (*E. tristicolor* holotype ♀ [ANSP, catalog number: 10123]).

USA: **Utah:** Logan, 14.vii.1922, E.P. Van Duzee (*E. rufomaculatus* holotype ♀ [CAS, catalog number: 01609]); **Washington:** Pullman, 02.viii.1908, W.M. Mann (*E. humillimus* holotype ♂ [USNM, catalog number: 534047]); Olympia, 02.vii.1896, T. Kincaid (*E. olympiellus* holotype ♂ [USNM, catalog number: 534051]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAC6215. Specimens examined and sequenced.—USA: **California:** 2♀, 4♂ (PCYU); **Colorado:** 2♀, 1♂ (PCYU); **Idaho:** 5♀ (PCYU); **Oregon:** 2♀, 1♂ (PCYU); **Washington:** 1♂ (PCYU); **Wyoming:** 2♀ (AMNH, BBSL).

**Non-barcoded material examined.** Canada: **British Columbia:** 5♀, 5♂ (CNC).

USA: **California:** 4♀, 2♂ (PCYU); 17.2 mi S Livermore (on Mines Road, Alameda County), 22.v.1976, M.L. Siri and R.B. Kimsey (1♂, UCBME); Boca (Nevada County), 21.vi.1962, E.J. Montgomery (1♂, UCBME), 31.vii.1967, R.M. Bohart (1♂, UCBME); Carnelian Bay (Lake Tahoe), 24.vi.1973, R.M. Bohart (1♀, UCBME); Dollar Lake Trail (San Bernardino Mountains), 11.vii.1966, R.M. Bohart (1♂, UCBME); Hwy 99, 1.7 mi S Hwy 223 (Kern County), 16.ix.1999, G.R. Ballmer (1♀, UCR); **Colorado:** 3♀, 4♂ (PCYU); 6 mi ESE Kremmling (Grand County), 20.vii.1982, P. Robinson (1♀, CUM); **Idaho:** 6♀ (PCYU); Grasmere (Owyhee County), 07.vii.1968, A.R. Gittins (1♂, UCBME); Ketchum (43.7630° N; 114.4003° W) (Blaine County), 25.vi.2007, J. Gibbs (1♀, JBWM); **Nevada:** Mount Rose Summit (Washoe County), 09.vii.1964, R.M. Bohart (1♂, UCBME); **Oregon:** 1♀, 1♂ (PCYU); Hwy 26 (44.5500° N; 120.3472° W) (Wheeler County), 28.vi.2007, J. Gibbs (1♀, JBWM).

**37. *Epeolus packeri* new species**

Figs 77, 78, 92D, & 97A

**Diagnosis.** The following morphological features in combination can be used to tell *E. packeri* apart from all other North American *Epeolus*: the pronotal collar is predominantly ferruginous; the axilla is large, with the tip extending as far back as or beyond the posterior margin of the mesoscutellum, dilated laterally, and like the mesoscutellum ferruginous; the mesopleuron is closely (most i<1d) and evenly punctate; the metasomal terga have pale but not brownish orange pubescence; and the T1–T3 apical fasciae are interrupted medially and commonly reduced to discrete lateral patches. *Epeolus packeri* resembles *E. andriyi*, *E. deyrupi*, *E. floridensis*, and *E. howardi* in that the axilla is large, with the lateral margin arcuate, and like the mesoscutellum ferruginous, and that the T1–T3 apical fasciae are interrupted medially. However, in *E. packeri* the pseudopygidial area of the female is wider (the apex >2 × the medial length) than in *E. andriyi*, *E. floridensis*, or *E. howardi* (the apex <2 × the medial length), and the T1 basal fascia is absent or reduced to a pair of small patches of pale tomentum whereas in *E. andriyi*, *E. floridensis*, and *E. howardi* T1 has a distinct, although often medially-interrupted, basal fascia. *Epeolus packeri* closely resembles *E. deyrupi*, but in *E. deyrupi* the mesopleuron commonly has sparser punctures ventrolaterally (i≤2d) than that of *E. packeri*, with the interspaces shining or somewhat dull due to tessellate surface microsculpture, and the T1–T3 apical fasciae are (to varying degrees) brownish orange medially and off white laterally. *Epeolus packeri* is also similar to *E. scutellaris*, but in *E. scutellaris* the pronotal collar is predominantly black and the T1–T3 apical fasciae are complete or only very narrowly interrupted medially.

**Description.** FEMALE: Length 8.3 mm; head length 2.0 mm; head width 2.8 mm; fore wing length 6.2 mm.

*Integument coloration*. Black in part, at least partially ferruginous on mandible, labrum, lower paraocular area, antenna, pronotal collar, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, metanotum, mesopleuron, metapleuron, propodeum, legs, and metasomal sterna. Mandible with apex darker than rest of mandible; preapical tooth slightly lighter than mandibular apex (difficult to see in holotype; described from paratype). Antenna brown except scape, pedicel, and F1 extensively orange. F2 with orange spot basally. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum reddish orange except medially on anterior margin and along

parapsidal line. Wing membrane dusky subhyaline, slightly darker at apex. Legs more extensively reddish orange than brown or black.

*Pubescence*. Face with tomentum densest on paraocular area around antennal socket, otherwise almost entirely bare. Mesoscutum without pale tomentum. Dorsum of metasoma with bands of off-white short appressed setae. Mesopleuron nearly bare, except along margins. Metanotum with tomentum uninterrupted except for median bare patch in posterior half, uniformly off white. T1 and T2 with apical fasciae medially interrupted, narrowed (broader laterally), and removed from apical margin; T2 with fascia without anterolateral extensions of tomentum. Metasoma otherwise without fasciae, although T3 and T4 with few sparsely scattered pale hairs present on apical impressed areas. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on flat disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 1/3 MOD.

*Surface sculpture*. Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate matte spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate posteriorly (i=1–2d), sparsely punctate (i>2d) to impunctate anteriorly and along margins. Mesopleuron with ventrolateral half densely punctate (i≤1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure*. Preapical tooth blunt and obtuse. Labral apex with pair of small denticles, each preceded by longitudinal carina. Frontal keel not strongly raised. Scape with greatest length 1.9 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by less than 1 MOD at its terminal (difficult to see in holotype; described from paratype). Mesoscutellum moderately bigibbous. Axilla large, its lateral margin (L) more than half as long as mesoscutellar width (W) (L/W ratio = 0.7) and tip extending slightly beyond apex of horizontal dorsal portion of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 the medial length of axilla; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: face with more abundant pale tomentum, densest from midlength of clypeus to upper paraocular and frontal areas; F2 shorter, but still longer than wide (L/W ratio = 1.2); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered basally and sparser apically, with the interspaces shining.

**Etymology.** This species is named in honor of my dissertation adviser, Prof. Laurence Packer, who collected the first specimen of this species I have seen.

**Distribution:** Florida peninsula (Fig. 78).

**Ecology.** HOST RECORDS: The host species of *E. packeri* is/are presently unknown.

FLORAL RECORDS: Labels of examined voucher specimens indicate a floral association with *Solidago*.

**Discussion.** In Mitchell's (1962) keys to female and male *Epeolus*, this species comes out as *E. floridensis* in which T1 is not bright ferruginous but black. However, in *E. floridensis* the dorsum of the mesosoma and metasoma has more abundant pale pubescence, and the pseudopygidial area is conspicuously narrower. Moreover, all examined specimens of *E. floridensis* (adults) were collected in spring whereas all those identified as *E. packeri* were collected in October.

In terms of surface sculpture, structure, and the width of the pseudopygidial area, *E. packeri* is most similar to *E. scutellaris*, and sequenced representatives of both forms share the same BIN. The two are considered to be heterospecific based on the marked abundance of red coloration coupled with a loss of pubescence (the same rationale for treating *E. glabratus* as distinct from *E. lectoides*) in *E. packeri*, features that are common in Florida Hymenoptera and constitute an unexplained regional phenomenon (Deyrup and Eisner 2003).

**Material studied. Type material.** Primary: USA: **Florida:** Homosassa Tract (Citrus County), 19.x.2002, J. Mosley (holotype ♀, FSCA).

Secondary: USA: **Florida:** Butterfly Garden W McGuire Center for Lepidoptera Research (Gainesville, Alachua County), 20.x.2009, C. Whitehill (paratypes 2♂, FSCA);

Gainesville (Alachua County), 14.x.2012, S. Lenberger (paratype ♂ [CCDB-30383 D04], FSCA); Gainesville (Paynes Prairie, Alachua County), 13-23.x.1997, L. Masner (allotype ♂, PCYU); Homosassa Tract (Citrus County), 19.x.2002, J. Mosley (paratypes 1♀, 1♂, ABS); W Murdoch, 20.x.1983, L. Packer (paratype ♀, PCYU); Withlacoochee State Forest (Citrus County), 19.x.2002, J. Mosley (paratypes 2♂, ABS).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAG5250. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**38. *Epeolus pusillus* Cresson, 1864**

Figs 79, 80, & 98A

*Epeolus pusillus* Cresson, 1864b. Proc. Entomol. Soc. Phil. 2: 398 (♀).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. pusillus* apart from all other North American *Epeolus* except *E. basili, E. nebulosus*, and *E. novomexicanus*: the axilla is large, with the tip extending well beyond the midlength of the mesoscutellum but at most to the band of pale tomentum along its posterior margin, dilated laterally, and usually ferruginous to some degree (rarely all black) whereas the mesoscutellum is entirely black; the axilla's free portion is clearly less than 2/5 as long as its entire medial length; the mesopleuron is closely (most i<1d) and evenly punctate, that of the female is obscured by white tomentum only in the upper half (with a large, sparsely hairy circle occupying much of the ventrolateral half) whereas that of the male (excluding the hypoepimeral area) is entirely obscured by white tomentum; the T1–T3 apical fasciae are complete or only very narrowly interrupted medially; the T2 fascia has lobe-like anterolateral extensions of tomentum; and the pseudopygidial area of the female is lunate and wider than long (the apex ≤2 × the medial length). *Epeolus basili, E. nebulosus*, *E. novomexicanus*, and *E. pusillus* are all extremely similar to one another. Whereas in *E. basili* the flagellum, at least ventrally, is the same reddish-orange color as the legs (tibiae to tarsi) as are usually the metasomal sterna, in *E. pusillus* the flagellum, except sometimes F1, and metasomal

sterna are consistently brown or black and clearly not the same reddish-orange color as the legs (tibiae to tarsi). Whereas in *E. nebulosus* and *E. novomexicanus* the longitudinal extent of the T1 discal patch is less than or equal to the breadth of the apical fascia and the T2–T4 fasciae are on or very little removed from the apical margin and more or less evenly broad, in *E. pusillus* the longitudinal extent of the T1 discal patch is no less (and usually greater) than the breadth of the apical fascia and the T1–T3 apical fasciae are removed from the apical margin and commonly narrowed or narrowly interrupted medially. *Epeolus pusillus* is also similar to *E. scutellaris* in that the axilla is large, with the lateral margin arcuate, and that the apical fasciae are complete or only very narrowly interrupted medially. However, in *E. scutellaris* the pseudopygidial area of the female is much wider (the apex ~2.5–3 × the medial length) than in *E. pusillus*, and the mesopleuron of both the female and male is obscured by white tomentum only in the upper half (with a large, sparsely hairy circle occupying much of the ventrolateral half). Despite the species name '*pusillus*', meaning very small in Latin, the size range overlaps too much with other species to be diagnostic.

**Description.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Eastern North America to Mexico (Fig. 80).

**Ecology.** HOST RECORDS: Rozen and Favreau (1968) associated *E. pusillus* with *C. compactus compactus* Cresson based on observations of a female of the former entering and emerging from a nest of a female of the latter and subsequent discovery of an *Epeolus* egg upon excavation of the nest. Ascher et al. (2014) noted that the small size and flight season of *E. pusillus* suggest and additional or alternative association with *C. americanus* Cresson.

FLORAL RECORDS: See Onuferko (2017). Floral associations are also indicated in Suppl. material 1, which includes newly discovered associations with *Callirhoe involucrata* (Torr. & A. Gray) A. Gray (Malvaceae), *Heterotheca subaxillaris*, *Rudbeckia fulgida* Aiton, and *R. hirta* based on labels of examined voucher specimens.

**Discussion.** In Onuferko (2017), barcoded specimens from Utah were regarded as *E. pusillus*, but are now considered to be *E. novomexicanus*, with sequenced representatives of both species

sharing the same BIN. Detailed morphological and taxonomic remarks about this species are given in Onuferko (2017).

**Material studied. Type material.** Primary: USA: **Massachusetts:** F.G. Sanborn (holotype ♀ [ANSP, catalog number: 2228]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAX7180. Specimens examined and sequenced.—Canada: **Ontario:** 1♂ (PCYU).

USA: **Alabama:** Autauga County (32.4345° N; 86.5817° W), 19.x.2016, C.H. Ray (1♂, AUMNH); Lee County (32.5553° N; 85.3747° W), 11.x.2016, C.H. Ray (1♂, AUMNH); **Maryland:** 1♂ (BIML); **North Carolina:** 1♂ (BIML); **South Carolina:** Aiken Savannah River Site (33.3594° N; 81.6652° W), 30.ix.2016, S. McCann (1♂, JBWM); S Murrells Inlet, 04.x.2016, T.M. Onuferko (1♀, PCYU).

**Non-barcoded material examined.** Canada: **Ontario:** 13♀, 23♂ (CNC, DEBU, PCYU, ROM); Caledon (Forks of the Credit Provincial Park), 03.ix.1969, P. MacKay (1♀, PCYU); King, 13.vii.2000, J. Grixti (1♀, PCYU), 23.viii.2002, A. Gravel (1♀, PCYU); Norfolk County (42.6369° N; 80.5472° W), 03.ix.2008, A. Taylor (1♀, PCYU); Norwood, 24.viii.1982, T.D. Galloway (1♀, JBWM); Osprey Marsh (Frontenac County), 03.xi.2001 (1♀, PCYU); Queen's University Biological Station, 03.ix.2001 (1♀, PCYU); **Quebec:** 1♀ (CNC).

Mexico: **Chihuahua:** 17 mi N Chihuahua, 25.viii.1965, A. Raske (1♀, EMEC); Cuiteco, 14.ix.1969, T.A. Sears, R.C. Gardner, and C.S. Glaser (1♂, UCBME); **Sinaloa:** Mazatlán, 06.viii.1964, W.R.M. Mason (1♀, CNC), 27.iii.1979, L.D. French (1♀, UCBME), 28.iii.1979, L.D. French (1♂, UCBME).

USA: **Alabama:** Auburn (32.5701° N; 85.4603° W) (Lee County), 18.x.2014, C.H. Ray (1♂, AUMNH); Lee County (32.5553° N; 85.3747° W), 11.x.2016, C.H. Ray (1♂, AUMNH); **Florida:** 1♂ (AMNH); Alachua (Alachua County), 05.v.1974, E.E. Grissell (1♀, UCBME), 29.iv.1974, E.E. Grissell (2♀, UCBME); St. Andrews State Park (Panama City), 14.x.2000, C. Porter and L. Stange (1♀, 3♂, FSCA); **Illinois:** 1♀ (FMNH); **Indiana:** 1♂ (USNM); **Kansas:** Riley County (1♂, USNM); **Maryland:** 2♀, 8♂ (BIML); **Massachusetts:** 2♀, 4♂ (BIML); **Mississippi:** 1♂ (AMNH); **New Jersey:** 1♀ (AMNH); Seaside Park, Weiss and West (1♀,

CNC); **New York:** 2♀ (AMNH); **Oklahoma:** 1♂ (USNM); Lake Texoma (2 mi E Willis), vii.1965, R.M. Bohart (1♀, UCBME); **South Carolina:** 1♀, 1♂ (BIML, DEBU); **Texas:** 17 mi N Vernon (Wilbarger County), 02.iv.1979, R.J. McGinley (1♂, USNM); Canyon (Randall County), 21.vi.1969, R.M. Bohart (1♀, UCBME); Cotulla, 12.v.1906, J.C. Crawford (1♂, USNM); Dickinson (Galveston County), vi.1929, F.M. Hull (1♀, CNC); Lee County (1♂, USNM); Lick Creek Park (College Station, Brazos County), 22.ix.1990, J. Woolley and J. Huber (1♂, CNC); Stengl "Lost Pines" Biological Research Station (30.0800° N; 97.1830° W), 16.v.2013, J.L. Neff (1♂, CTMI); Victoria, 01.iv.1907, J.D. Mitchell (1♂, USNM).

**39. *Epeolus rufulus* Cockerell, 1941**

Figs 81, 82, & 96B

*Epeolus rufulus* Cockerell, 1941. Can. Entomol. 73: 36 (♀).

**Diagnosis.** The following morphological features in combination can be used to tell *E. rufulus* apart from all other North American *Epeolus* except *E. attenboroughi*: the mandible has a blunt, obtuse preapical tooth; the preoccipital ridge does not join the hypostomal carina; the mesoscutum is covered in pale tomentum, which is densest anteromedially; the axilla is elongate, extending well beyond the midlength of the mesoscutellum but not as far back as its posterior margin, and the free portion is distinctly hooked; the mesopleuron is closely (most i<1d) and evenly punctate; and T1–T4 have complete apical fasciae. Whereas in *E. attenboroughi* T1 has a comparatively narrow discal patch (the longitudinal band is more than half as wide as the breadth of the apical fascia in dorsal view) and in females F2 is not noticeably longer than wide, in *E. rufulus* the discal patch is so wide that the longitudinal band is barely visible in dorsal view and in females F2 is more than 1.2 × as long as wide. *Epeolus rufulus* is also similar to *E. ainsliei* in that in both species the axilla is dilated laterally and the free portion is distinctly hooked, and the T1–T4 apical fasciae are complete; however, in *E. ainsliei* the mandible is simple, the preoccipital ridge joins the hypostomal carina, and the mesoscutum has distinct paramedian bands.

**Redescription.** FEMALE: Length 7.6 mm (difficult to gauge in holotype because head detached and glued to collection label, and much of pronotum missing; given instead for non-type specimen most similar in size); head length 1.9 mm; head width 2.6 mm; fore wing length >5.1 mm (margins of both very worn in holotype).

*Integument coloration*. Black in part, at least partially ferruginous on mandible, labrum, clypeus, antenna, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, metanotum, mesopleuron, metapleuron, propodeum, legs, metasomal terga (including pygidial plate), and metasomal sterna. Mandible with apex darker than all but extreme base; preapical tooth lighter than mandibular apex (difficult to see in holotype; described from non-type specimen). Antenna brown and orange in part. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum orange along lateral margin and with pair of orange markings near posterior margin between midline and parapsidal line. Wing membrane subhyaline, apically dusky. Legs entirely reddish orange (both forelegs missing in holotype, but entirely reddish orange in non-type specimens).

*Pubescence*. Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum sparsely covered in pale tomentum. Mesopleuron with upper half sparsely hairy; ventrolateral half nearly bare, except along margins. Metanotum with tomentum rubbed off medially in holotype, but uninterrupted and uniformly off white in non-type specimens. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally. T1 with basal and apical fasciae and T2–T4 with apical fasciae complete, those of T2 and T3 somewhat broader laterally, T2 with fascia without anterolateral extensions of tomentum. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~2/5 MOD.

*Surface sculpture*. Punctures dense. Labrum and clypeus with punctures equally dense (i<1d). Impunctate spot lateral to lateral ocellus absent. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i<1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure*. Preapical tooth blunt and obtuse. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.9 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.6). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal (not visible in holotype because head detached and glued to collection label; described from non-type specimens). Mesoscutellum weakly bigibbous. Axilla large, its lateral margin (L) more than half as long as mesoscutellar width (W) (L/W ratio = 0.6) and tip extending well beyond midlength of mesoscutellum but not as far back as its posterior margin; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin arcuate and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, as long as wide (L/W ratio = 1.1); mesopleuron almost entirely obscured by white tomentum; S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep, well-separated punctures, with the interspaces shining.

**Distribution:** Great Plains to American southwest and presumably Mexico, given the close proximity of one collection locality (near Cloverdale, New Mexico) to the Mexico–United States border (Fig. 82).

**Ecology.** HOST RECORDS: The host species of *E. rufulus* is/are presently unknown.

FLORAL RECORDS: The label of one examined voucher specimen indicates a floral association with *Heterotheca subaxillaris* ssp. *latifolia*.

**Discussion.** In his unpublished thesis, Brumley (1965) synonymized *Epeolus rufulus* under *E. crucis*, treating the latter as a valid species. Herein, *E. crucis* is synonymized under *E. compactus* for reasons described in the Discussion of *E. compactus*. Also synonymized under *E. crucis* was *E. novomexicanus*, but morphological comparisons suggest that the type of *E. novomexicanus* belongs to the "*pusillus* group". *Epeolus rufulus* is similar in overall appearance to *E. ainsliei* and *E. attenboroughi*, and the ranges of the three species overlap to some extent.

*Epeolus rufulus* appears to be uncommon, or at least uncommonly collected. The male of *E. rufulus* is described here for the first time. There is very little morphological variation among the few examined specimens, and in all the mesoscutum lacks distinct paramedian bands and is instead sparsely covered in pale tomentum.

**Material studied. Type material.** Primary: USA: **Colorado:** Crowley, 01.ix.1932, M.T. James (holotype ♀ [CUM, catalog number: 0000043]).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ADI5469. Specimens examined and sequenced.—USA: **Colorado:** Stratton (39.2645° N; 102.6681° W) (Kit Carson County), 22.viii.2014, A. Carper (1♂, CUM).

**Non-barcoded material examined.** USA: **Kansas:** Finney (37.9411° N; 100.8811° W) (3.2 km S Garden City), 13.ix.2001, R.W. Brooks (1♀, KUNHM); **Nebraska:** 2 mi S Alliance (Box Butte County), 13.viii.1959, W.E. LaBerge (1♂, BBSL); **New Mexico:** ~6 mi E Cloverdale (31.4250° N; 108.8144° W) (Hidalgo County), 21.viii.2004, D. Yanega (1♀, UCR).

**40. *Epeolus scutellaris* Say, 1824**
Figs 83, 84, & 97C

*Epeolus scutellaris* Say, 1824. In Keating, Narr. Long's 2nd Exped., v. 2: 355 (♀); Onuferko, 2017. Can. J. Arthropod Identif. No 30: 44 (♀) [neotype designation].
*Epeolus vernoniae* Cockerell, 1907a. Entomologist 40: 136 (♂).

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. scutellaris* apart from all other North American *Epeolus*: the pronotal collar is predominantly black; the axilla is large, with the tip extending to or beyond the band of pale tomentum along the posterior margin of the mesoscutellum, dilated laterally, and ferruginous to some degree whereas the mesoscutellum ranges from entirely black to entirely ferruginous; the mesopleuron is closely (most i<1d) and evenly punctate and obscured by white tomentum only in the upper half (with a large, sparsely

hairy circle occupying much of the ventrolateral half); the T1–T3 apical fasciae are complete or only very narrowly interrupted medially; and the pseudopygidial area of the female is lunate with the apex clearly >2 × the medial length. *Epeolus scutellaris* resembles *E. basili*, *E. nebulosus*, *E. novomexicanus*, and *E. pusillus* in that the axilla is large, with the lateral margin arcuate, and that the apical fasciae are complete or only very narrowly interrupted medially. However, in *E. scutellaris* the pseudopygidial area of the female is wider (the apex ~2.5–3 × the medial length) than in the four members of the "*pusillus* group" (the apex clearly <2.5 × the medial length). In all four members of the "*pusillus* group", the mesopleuron of the male (excluding the hypoepimeral area) is entirely obscured by white tomentum and lacks the sparsely hairy circular area present in both sexes of *E. scutellaris*. *Epeolus scutellaris* is most similar to *E. packeri* in terms of surface sculpture and structure, but in *E. packeri* the pronotal collar is predominantly ferruginous, the T1 basal fascia is absent or reduced to a pair of small patches of pale tomentum, and the T1–T3 apical fasciae are interrupted medially and commonly reduced to discrete lateral patches. *Epeolus scutellaris* is also similar to *E. andriyi* and *E. howardi*, but in *E. andriyi* and *E. howardi* the T1–T3 apical fasciae are distinctly interrupted medially, and the pseudopygidial area of the female is lunate with the apex <2 × the medial length.

**Description.** This species was recently redescribed (Onuferko 2017).

**Distribution:** Widely distributed across the contiguous United States, excluding peninsular Florida and the west coast, and southern Canada (Maritime to Prairie provinces) (Fig. 84).

**Ecology.** See Onuferko (2017) for host and floral records. Floral associations are also indicated in Suppl. material 1, which includes newly discovered associations with *Chrysothamnus* (possibly in reference to plants that now are in the genus *Ericameria*), *Erigeron*, and *Heterotheca subaxillaris* based on labels of examined voucher specimens.

**Discussion.** In Onuferko (2017), *E. scutellaris* is said to be similar to two species from Florida yet to be formally recognized, which herein are formally described under the names *Epeolus deyrupi* and *E. packeri*. Detailed morphological and taxonomic remarks about this species are given in Onuferko (2017).

**Material studied. Type material.** Primary: USA: **New York:** Keene Valley (Essex County), 12.viii.1917, H. Notman (*E. scutellaris* neotype ♀, AMNH); **Virginia:** Falls Church, 04.ix.????, N. Banks (*E. vernoniae* holotype ♂, AMNH).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:AAG5250. Specimens examined and sequenced.—Canada: **Nova Scotia:** 1♀ (RSKM); **Ontario:** 1♀, 1♂ (PCYU).

USA: **Alabama:** Autauga County (32.4345° N; 86.5817° W), 19.x.2016, C.H. Ray (1♂, AUMNH); Lee County (32.5553° N; 85.3747° W), 09.x.2016, C.H. Ray (1♀, AUMNH); Montgomery (32.3135° N; 86.1744° W) (Montgomery County), 01.x.2016, A. Jeon (1♀, AUMNH); **Idaho:** 2♂ (AMNH).

**Non-barcoded material examined.** Canada: **Manitoba:** Canadian Forces Base Portage la Prairie, 03.ix.1974, T.D. Galloway (2♀, JBWM); **New Brunswick:** 1♀, 1♂ (CNC); **Nova Scotia:** 11♀, 8♂ (CNC, PCYU, RSKM); Brooklyn Street (near Kentville, Kings County), 15.ix.2005, C. Sheffield and S. Westby (1♀, PCYU); Port Hawkesbury Station (Cape Breton Island), 03.ix.1985, L. Packer (1♀, PCYU); **Ontario:** 29♀, 29♂ (CNC, PCYU, ROM); Lambton County, 29.viii.2007, A. Taylor (1♀, PCYU); Marshlands Conservation Area (Kingston, Frontenac County), 20.viii.2016, J. Gibbs (2♀, JBWM); Norwood, 24.viii.1982, T.D. Galloway (1♀, JBWM); Ottawa Airport, 03.ix.1985, L. Packer (1♀, PCYU); Rockwood, 22.ix.1972, T.D. Galloway (1♀, JBWM); **Quebec:** 3♀, 2♂ (CNC).

USA: **Alabama:** Auburn (32.6005° N; 85.5102° W) (Lee County), 15.x.2016, C.H. Ray (1♀, AUMNH); Autauga County (32.4345° N; 86.5817° W), 19.x.2016, C.H. Ray (1♀, AUMNH); Covington County (31.2550° N; 86.2887° W), 05.xi.2016, C.H. Ray (2♀, AUMNH); Lee County (32.5553° N; 85.3747° W), 09.x.2016, C.H. Ray (3♀, AUMNH); Mobile Botanical Gardens (30.7010° N; 88.1606° W) (Mobile County), 27.ix.2016, C.H. Ray (1♂, AUMNH); **Arizona:** 17 mi S Safford, 22.viii.1986, R.R. Snelling (1♂, LACM); 4 mi E Willcox (Cochise County), 28.viii.1985, J.G and B.L. Rozen (2♂, AMNH); 5 mi S Apache (Cochise County), 12.ix.1976, R.M. Bohart (1♂, UCBME); 5 mi W Portal (Cochise County), 31.viii.2003, J.S. Ascher (1♂, AMNH); Near Portal (Cochise County), 08.ix.2011, A. Payne (1♀, AMNH);

Phoenix (Maricopa County), 13.x.1997, K.C. Rozen (1♂, AMNH); W Turkey Creek (Chiricahua Mountains), 02.ix.2003, J.G. Rozen, J.S. Ascher, R.L. Staff, and R.E. Edwards (1♀, AMNH); **Colorado:** 2.4 mi N Hooper (Saguache County), 24.viii.1967, R.R. Snelling (1♂, LACM); **Maine:** 2♀, 1♂ (BIML); **Maryland:** 4♂ (BIML); **Michigan:** 1♀ (BIML); East Lansing (Ingham County), 03.ix.2016, J. Gibbs (1♂, JBWM); **Minnesota:** 3 mi E Glyndon (Clay County), 15.ix.1986, J.R. Powers (1♂, EMEC); Wabasha (Wabasha County), 17.viii.1995, J.R. Powers (2♀, 5♂, EMEC); **New Hampshire:** North Conway, Bequaert (1♂, EMEC); **New Jersey:** 1♂ (AMNH); **New Mexico:** 17 mi S Animas (Hidalgo County), 24.viii.1994, J.G. Rozen and J.S. Ascher (1♂, AMNH); 17 mi S Animas (Hidalgo County), 30.viii.1994, J.G. Rozen and J.S. Ascher (1♀, AMNH); 26 mi S Animas (Hidalgo County), 22.viii.1997, J.G. Rozen and B. McAdams (1♂, AMNH); 27-32 mi S Animas (Hidalgo County), 24.viii.1994, J.G. Rozen and J.S. Ascher (1♂, AMNH); 29-31 mi S Animas (Hidalgo County), 30.viii.1994, J.G. Rozen and J.S. Ascher (1♂, AMNH); 3 mi S Rodeo (Hidalgo County), 07.ix.2003, J.S. Ascher (1♂, AMNH); Cienega (Hidalgo County), 28.viii.1997, J.G. Rozen and B. McAdams (1♂, AMNH); Rodeo (Hidalgo County), 07.ix.1976, R.M. Bohart (1♂, UCBME); U.S. Route 180 (11 mi SE Mangas, Grant County), 04.ix.2011, J.G Rozen and E.S. Wyman (1♂, AMNH); **New York:** Cornell Botanic Gardens (42.4497° N; 76.4711° W) (Cornell University, Tompkins County), 19.viii.2012, J. Gibbs (1♀, JBWM); Lime Hollow (42.5650° N; 76.2550° W) (Cortland County), 03.ix.2011, J. Gibbs (1♀, JBWM); Mundy Wildflower Garden (42.4510° N; 76.4690° W) (Cornell University, Tompkins County), 18.viii.2012, J. Gibbs (1♂, JBWM); **North Carolina:** 1♂ (AMNH); **North Dakota:** 1 mi SE McLeod (Ransom County), 19.viii.1988, J.R. Powers (1♀, EMEC), 10.ix.1997, J.R. Powers (1♀, EMEC); 11 mi W Walcott (Richland County), 08.ix.1987, J.R. Powers (2♀, EMEC), 02.ix.1996, J.R. Powers (1♀, EMEC); 7 mi SE Sheldon (Ransom County), 19.viii.1980, J.R. Powers (2♀, 1♂, EMEC), 28.viii.1981, J.R. Powers (1♀, EMEC), 09.viii.2000, J.R. Powers (1♂, EMEC), 26.vii.1985, J.R. Powers (1♂, EMEC); **Pennsylvania:** Wilawana, 08-10.1934, R.H. Crandall (1♂, LACM); **Utah:** Cornish (Cache County), 04.ix.1982, R.M. Bohart (1♀, UCBME); **Vermont:** 1♀, 2♂ (AMNH); **Wisconsin:** 1♀ (FMNH).

**41. *Epeolus splendidus* new species**

Figs 85, 86, & 102A

*Epeolus politus* Brumley, 1965. M.S. thesis, Utah State University, Logan 60 (♀) [*nomen nudum*].

**Diagnosis.** The following morphological features in combination can be used to tell *E. splendidus* apart from all other North American *Epeolus*: the propodeum (except the textured metapostnotum) is highly polished and (except along the lateral margins) hairless, and T1 has a complete white basal fascia whereas T1–T4 have complete bright yellow apical fasciae. As in *E. canadensis*, *E. compactus*, and *E. ferrarii*, in *E. splendidus* the mesoscutum has a small anteromedial patch of tomentum, although it is bright rather than pale yellow. However, in *E. splendidus* T1 lacks a distinct black discal patch and in females F2 is shorter, as long as wide. In all four species, the axilla does not attain the midlength of the mesoscutellum, and the axilla (except sometimes the tip) and mesoscutellum are black.

**Description.** FEMALE: Length 8.4 mm; head length 2.1 mm; head width 3.0 mm; fore wing length 6.6 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, legs, metasomal terga (including pygidial plate), and metasomal sterna. Mandible with apex and preapical tooth darker than rest of mandible. Antenna brown except scape and pedicel orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs with brown or black more extensive than reddish orange.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white and bright yellow short appressed setae. Pronotal collar with tomentum sparser medially, uniformly bright yellow. Mesoscutum with anteromedial chevron-shaped patch of bright yellow tomentum. Mesopleuron with upper half densely hairy, except beneath base of fore wing (hypoepimeral area); ventrolateral half sparsely hairy. Metanotum with tomentum uninterrupted, uniformly off white. T1 with broad, off-white basal fascia, complete bright yellow apical fascia, and narrow and extremely short discal patch of dark brown tomentum. T2–T4 each with complete bright yellow fascia, T2 and T3 with fasciae with anterolateral spots of sparser off-white tomentum. T5 covered in off-white tomentum except for

line of separation from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on flat disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~2/5 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with ventrolateral half densely punctate (i≤1d) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Labrum with pair of small subapical denticles, each preceded by small discrete longitudinal ridge. Frontal keel not strongly raised. Scape with greatest length 1.9 × greatest width. F2 as long as wide (L/W ratio = 1.0). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum weakly bigibbous. Axilla small to intermediate in size, its lateral margin (L) less than half as long as mesoscutellar width (W) (L/W ratio = 0.3) and tip not extending beyond midlength of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 1/3 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, nearly as long as wide (L/W ratio = 0.95); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered basomedially and sparser apically and laterally, with the interspaces shining.

**Etymology.** The name is in reference to the uniquely smooth, shiny propodeum of this species. From the Latin, “splendidus” (bright).

**Distribution:** Known to occur in all major hot North American deserts (Fig. 86).

**Ecology.** HOST RECORDS: The female PCYU paratype (see Material studied) was collected in the spring of 2015 along the Catalina Highway in Pima County, Arizona, USA where possible

host *Colletes* visiting *Eriogonum* Michx. were collected and observed. Using Stephen's (1954) key, collected females were identified as *C. wootoni* Cockerell (one of which was sequenced and assigned the same BIN [BOLD:AAI9255] as a male from New Mexico whose terminalia were excised for identification) whereas collected males (one of which was sequenced and assigned the following BIN: BOLD:ABZ4837) were identified (based in part on examination of the terminalia, which were excised) as *C. eulophi*.

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Baileya* Harv. & A. Gray ex A. Gray, *Encelia farinosa* A. Gray ex Torr. (Compositae), *Eriogonum inflatum* Torr. & Frém., *Larrea* Cav., *Parkinsonia* L. (Leguminosae), and *Prosopis velutina*, and BugGuide (http://www.bugguide.net/) indicates an association with *Erigeron*.

**Discussion.** This southwestern species was identified as unique by Brumley (1965), and the colors and patterns of pubescence on the mesosoma and metasoma clearly set it apart from other *Epeolus* in North America. There is very little morphological variation among examined specimens, and sequenced material was assigned the same BIN. Based on known records, adults of *E. splendidus* are active in spring.

**Material studied. Type material.** Primary: USA: **Arizona:** Usery Mountains (Mesa, Maricopa County), iv.2009, J. Alcock (holotype ♀ [CCDB-28230 D07], AMNH).

Secondary: Mexico: **Durango:** Reserva de la Biósfera de Mapimí (26.6803° N; 103.7408° W), 24.iii.1995, R. López (paratype ♂, BBSL); **Jalisco:** Plan de Barrancas, 24.iii.1962, F.D. Parker (paratype ♂, UCBME).

USA: **Arizona:** 11 mi SW Congress (Yavapai County), 29.iv.1990, J.G. Rozen (paratype ♂, AMNH); 14 mi SW Apache (Cochise County), 22.v.1988, J.G. Rozen (paratype ♀, AMNH); 2 mi E Tanque Verde (Pima County), 14.iii.??54, F. Werner (paratype ♂, LACM); 20 mi NE Mesa (Maricopa County), 28.iv.1988, P. Robinson (paratype ♂, CUM); 8 km E Robles Junction (32.0667° N; 111.2500° W) (Tucson, Pima County), 15-27.iv.1996, D. Yanega (paratype ♀, UCR); Arizona-Sonora Desert Museum/Tucson Mountain Park (Pima County), 11-12.iv.1988, K. Krombein and B. Norden (paratypes 2♂, USNM); Catalina Hwy (32.3631° N; 110.7137° W) (Santa Catalina Mountains, Coronado National Forest), 29.v.2015, A.T. Onuferko (paratype ♀ [CCDB-22013 E11], PCYU); E Calle del Prado & N Palo Verde Ave (Tucson, Pima County),

09.iv.1997, R. Minckley (paratype ♂, BBSL); Mouth of Bear Canyon (Tucson, Santa Catalina Mountains), 29.iii.1964, F.G. Werner (allotype ♂, KUNHM); Nogales (Santa Cruz County), 20.iv.1967, P. Torchio and N. Youssef (paratype ♂, BBSL); Phoenix (33.6185° N; 111.9917° W) (Maricopa County), 17-19.iv.2009, J.G. Rozen (paratype ♀, AMNH); Sabino Canyon (near Tucson, Pima County), 03.iv.1972, B. Simpson (paratype ♂, LACM); Tucson (Pima County), 07.v.1987, J.G. Rozen (paratype ♀, AMNH); **California:** Clark Mountain (35.5217° N; 115.6428° W) (San Bernardino County), 23.v.2001, D. Yanega (paratype ♂, UCR); **Texas:** Alpine (Brewster County), 29.v.1952, M. Cazier, W. Gertsch, and R. Schrammel (paratype ♀, AMNH).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACX0474. See Type material for specimens examined and sequenced (indicated by unique CCDB-plate and well number).

**42. *Epeolus tessieris* new species**

Figs 87, 88, & 92H

*Epeolus cretus* Brumley, 1965. M.S. thesis, Utah State University, Logan 42 (♀) [*nomen nudum*].

**Diagnosis.** The following morphological features in combination can be used to tell *E. tessieris* apart from all other North American *Epeolus* except *E. interruptus*: the axilla does not attain the midlength of the mesoscutellum, its tip is unattached to the mesoscutellum for less than 1/3 of the entire medial length of the axilla, and like the mesoscutellum is ferruginous; the mesopleuron has sparser punctures ventrolaterally (most i≥1d) than in upper half, with the interspaces shining; and T1–T4 have medially-interrupted metasomal fasciae. Whereas in *E. interruptus* the metanotum has a blunt median process and T1 has a wide triangular discal patch with concave lateral sides, in *E. tessieris* the metanotum is flat and T1 has a trapezoidal to nearly semicircular discal patch.

**Description.** FEMALE: Length 5.8 mm; head length 1.7 mm; head width 2.3 mm; fore wing length 4.8 mm.

*Integument coloration.* Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, mesoscutellum, and legs. Mandible with apex darker than rest of mandible; preapical tooth lighter than mandibular apex (difficult to see in holotype because mandible closed; described from paratypes). Antenna brown and orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow short appressed setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, except beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum sparser medially, uniformly off white. T1 with median trapezoidal verging on semicircular black discal patch enclosed by pale tomentum, except for medial separations at base and apex. T2–T4 with fasciae interrupted medially and narrowed before becoming somewhat broader laterally, T2 with fascia with anterolateral extensions of sparser tomentum. T5 with two large patches of pale tomentum anterolateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by much more than 1/4 MOD.

*Surface sculpture.* Punctures dense, except those of mesopleuron. Labrum with larger punctures than clypeus, but punctures of both equally dense (i≤1d). Small impunctate shiny spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate (i≤2d). Mesopleuron with denser (i≤1d) punctures in upper half than ventrolateral half (i>1d, largely impunctate areas below line of pale tomentum), the interspaces shining. Metasomal terga with punctures very fine, dense (i≈1d), evenly distributed on disc.

*Structure.* Preapical tooth blunt and obtuse. Labrum with submedial pair of very small denticles, apex with pair of small points separated by shallow concavity (difficult to see in holotype; described from paratypes). Frontal keel not strongly raised. Scape with greatest length 1.8 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not

joining hypostomal carina, from which it is separated by about 1.5 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin (L) less than half as long as mesoscutellar width (W) (L/W ratio = 0.4) and not extending beyond midlength of mesoscutellum; axilla with tip visible, but unattached to mesoscutellum for less than 1/3 the medial length of axilla; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, not noticeably longer than wide (L/W ratio = 1.1); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered basomedially and sparser apically and laterally, with the interspaces shining.

**Etymology.** This species is named in honor of my wife, biologist Stéphanie Tessier. The name is in the genitive case and declined as *mulier*, a Latin noun with a consonant stem.

**Distribution:** Northern Mexico and bordering U.S. States (Fig. 88).

**Ecology.** HOST RECORDS: The host species of *E. tessieris* is/are presently unknown.

FLORAL RECORDS: Labels of examined voucher specimens indicate floral associations with *Cuscuta umbellata* Kunth (Convolvulaceae), *Marshallia* Schreb. (Compositae), and *Pectis papposa*.

**Discussion.** Of the *Epeolus* Brumley (1965) identified as new, this appears to be the least commonly collected species. Among examined specimens, there is notable variability in punctation density of the mesopleuron, but the smooth, shiny interspaces are usually greater than puncture diameters. Although BIN-compliant sequences are presently not available for *E. tessieris*, 421 bp sequences are available for two specimens (a female from Arizona, USA and a male from Coahuila, Mexico), and there is virtually no divergence (<1%) between the two. Moreover, these sequences do not cluster closely with any sequences from other *Epeolus* species in a NJ tree (Suppl. material 2).

**Material studied. Type material.** Primary: USA: **Arizona:** 3 mi W Marana (Pima County), 13.ix.1962, J.C. Bequaert (holotype ♀, CAS).

Secondary: Mexico: **Baja California Sur:** Playa El Coyote (26 km SSE Mulegé), 08.ix.1977, E. Fisher and R. Westcott (paratype ♂, CAS); **Coahuila:** 7 km SE Zapata, 25.viii.1991, J.G. Rozen (paratype ♂, KUNHM).

USA: **Arizona:** 1 mi E Douglas (Cochise County), 17.viii.1962, M.A. Cazier (paratype ♂, UCBME); 3 mi W Marana (Pima County), 13.ix.1962, J.C. Bequaert (allotype ♂, KUNHM); 4 mi E Willcox (Cochise County), 30.viii.2004, J.G. Rozen and J.S. Ascher (paratype ♀, AMNH); Tucson (Pima County), 27.x.1939, R.H. Crandall (paratype ♀, LACM); **New Mexico:** 1 mi N Rodeo (Hidalgo County), 22.viii.1964, J.H. Puckle, M.A. Mortenson, and M.A. Cazier (paratype ♂, EMEC); **Texas:** Kerrville, 31.v.??06, F.C. Pratt (paratype ♀, USNM).

**DNA barcoded material with BIN-compliant sequences.** Unavailable.

**43. *Epeolus zonatus* Smith, 1854**

Figs 89, 90, & 97H

*Epeolus zonatus* Smith, 1854. Cat. Hym. Brit. Mus. 2: 257 (♀, ♂), **new lectotype designation**

**Diagnosis.** The following morphological features in combination (excluding any that are specific to the opposite sex of the one being diagnosed) can be used to tell *E. zonatus* apart from all other North American *Epeolus* except *E. erigeronis, E. ilicis,* and *E. inornatus*: the mandible is simple; the axilla does not attain the midlength of the mesoscutellum but the free portion is distinctly hooked, with the tip unattached to the mesoscutellum for more than 1/3 of the entire medial length of the axilla; and the pseudopygidial area of the female is distinctly campanulate with the apex <2 × the medial length. Whereas in *E. erigeronis, E. ilicis,* and *E. inornatus* the pronotal collar and metasomal terga are black, as are sometimes the axilla and mesoscutellum, in *E. zonatus* the pronotal collar, axilla, mesoscutellum, T1, and T2 are ferruginous. Also, in *E. zonatus* the dorsum of the mesosoma and metasoma is commonly with much less pale pubescence.

**Redescription.** FEMALE: Length 9.7 mm; head length 2.3 mm; head width 3.1 mm; fore wing length 6.2 mm.

*Integument coloration.* Black in part, at least partially ferruginous on mandible, labrum, clypeus, antenna, pronotal collar, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, metanotum, mesopleuron, legs, T1, T2, and metasomal sterna. Mandible with apex darker than all but extreme base. Antenna brown and orange in part. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum reddish-brown along lateral margin and with pair of reddish-brown markings near posterior margin between midline and parapsidal line. Wing membrane dusky subhyaline, slightly darker at apex. Legs more extensively reddish orange than brown or black.

*Pubescence.* Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Mesoscutum without pale tomentum. Dorsum of metasoma with bands of off-white short appressed setae. Mesopleuron nearly bare, except along margins. Metanotum with tomentum sparser medially, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae at most only narrowly joined laterally (not joined in lectotype and multiple non-type specimens). T1 with basal and apical fasciae and T2–T3 with apical fasciae widely separated medially, the apical fasciae reduced to pairs of small patches somewhat broader laterally, T2 with fascia without anterolateral extensions of tomentum. T4 with fascia much more narrowly interrupted medially than on preceding terga. T5 with two faint patches of pale tomentum lateral to and contacting pseudopygidial area at apex, diverging from pseudopygidial area basally. T5 with pseudopygidial area campanulate, its apex less than twice as wide as medial length, indicated by silvery setae on impressed disc of apicomedial region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by ~2/5 MOD.

*Surface sculpture*. Punctures dense. Labrum with larger and sparser punctures (i=1–2d) than clypeus (i<1d). Small impunctate matte spot lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally (i<1d), less so laterally (i=1–2d). Mesopleuron with denser (i≤1d) punctures in upper half than ventrolateral half (i≤2d), the interspaces shining; mesopleuron with punctures similar in size throughout. Metasomal terga with punctures very fine, dense (i=1–2d), evenly distributed on disc; the interspaces shining somewhat.

*Structure*. Mandible without preapical tooth. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel not strongly raised. Scape with greatest length 1.9 × greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin (L) nearly half as long as mesoscutellar width (W) (L/W ratio = 0.4–0.5) and tip not extending beyond midlength of mesoscutellum; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin relatively straight and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, not noticeably longer than wide (L/W ratio = 1.1); S4 and S5 with much longer coppery to silvery subapical hairs; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

**Distribution:** Florida and coastal Georgia (Fig. 90).

**Ecology.** HOST RECORDS: The host species of *E. zonatus* is/are presently unknown.

FLORAL RECORDS: Mitchell (1962) indicated floral associations with *Crataegus* L. (Rosaceae) and *Prunus* L. Labels of examined voucher specimens further indicate associations with *Ambrosia artemisiifolia* L. (Compositae), *Aralia spinosa*, *Clinopodium ashei*, *Ilex cassine* L., *I. glabra*, *Licania michauxii*, *Persea borbonia* (L.) Spreng. (Lauraceae), *Prunus angustifolia*, and *Serenoa repens*.

**Discussion.** Smith (1854) described *E. zonatus* from both sexes, represented by three syntypes (all females) deposited at the NHMUK. The male description is actually based on a female specimen (see *E. zonatus* paralectotype [catalog number: 010812211] under Type material) of another species (*E. bifasciatus*). All three specimens were examined, and one of the two females of the true *E. zonatus* is herein designated as the lectotype, the one that is in better condition that fits Smith's (1854) original description of the female.

Structurally, *E. zonatus* and *E. ilicis* are identical, but in *E. zonatus* the pronotal collar, axilla, mesoscutellum, and discs of T1 and T2 are ferruginous, whereas in *E. ilicis* at least the pronotal collar and metasomal terga are entirely black. These are the exact same features that separate *E. glabratus* (another species restricted to peninsular Florida and coastal Georgia) from *E. lectoides*. Presently, only a single 422 bp sequence is available for *E. ilicis* (a male specimen from Florida, USA), which clusters with sequences of *E. zonatus* (Suppl. material 2), and all were assigned the same BIN. However, as the morphological differences between the two species are consistent, and because there appears to be little overlap in the ranges of both species, I have opted to treat *E. ilicis* and *E. zonatus* as heterospecific, despite the apparent lack of evidence of genetic divergence. This is another example of red-marked Hymenoptera in Florida with black congeners elsewhere (see Deyrup and Eisner 2003).

**Material studied. Type material.** Primary: USA: **Florida:** (*E. zonatus* lectotype ♀ [NHMUK, catalog number: 010812210]).

Secondary: USA: **Florida:** St. Johns Bluff (*E. zonatus* paralectotypes 2♀ (1 numbered [NHMUK, catalog number: 010812211])).

**DNA barcoded material with BIN-compliant sequences.** Available. BOLD:ACM5887. Specimens examined and sequenced.—USA: **Florida:** Archbold Biological Station (Highlands County), 17-23.iv.2007, S.M. Paiero (1♀, DEBU); **Georgia:** Cumberland Island National Seashore (30.8264° N; 81.4369° W) (Camden County), 02.iv.2012, D. Hoffman (1♀, RSKM).

**Non-barcoded material examined.** USA: **Florida:** A. Bolter (1♀, LACM); A.T. Solsson (1♂, AMNH); Alachua County, v.??49 (1♀, FMNH); Archbold Biological Station (Highlands County), 17-23.iv.2007, S.M. Paiero (1♂, DEBU); Archbold Biological Station (near Lake Annie, Highlands County), 14.iii.2016, M. Deyrup (1♂, ABS); Austin Cary Forest (Gainesville, Alachua County), 20.v.1976, G.B. Fairchild (1♀, UCBME); Dunedin (Pinellas County), 04.iv.1914 (2♀, AMNH); Gainesville (Alachua County), 02.iv.1976, W.H. Pierce (1♀, UCBME); Lake Louisa State Park (12 km S Clermont, Lake County), 05.iv.2014, K.A. Williams (2♀, FSCA); Lake Placid (Archbold Biological Station, Highlands County), 07.iv.1984, R.M. Bohart (2♂, UCBME); Leesburg (Lake County), 01-11.iii.1954, M. Statham (1♂, AMNH); N

FWC Carter Creek (27.5313° N; 81.4104° W) (Highlands County), 11.v.2010, J. Dunlap, M. and N. Deyrup, and K. Dearborn (2♂, ABS).

**Key to species of the genus *Epeolus* in Canada and the United States of America**

1 Axilla in dorsal view with tip extending to or beyond 2/3 the length of mesoscutellum (minimum posterior extent shown in Fig. 26D) (see also Figs 4D, 8D, 12D, 16D, 18D, 24D, 32D, 39D, 49D, 53D, 55D, 63D, 71D, 73D, 77D, 79D, 81D, 83D) ..... 2

\- Axilla in dorsal view with tip extending to less than 2/3 the length of mesoscutellum (maximum posterior extent shown in Fig. 20D) (see also Figs 6D, 10D, 14D, 22D, 28D, 30D, 34D, 36D, 41D, 43D, 45D, 47D, 51D, 57D, 59D, 61D, 65D, 67D, 69D, 75D, 85D, 87D, 89D) ..... 21

2 (1) Head with frontal area bearing pair of granulose protrusions, each located near upper mesal margin of compound eye (Fig. 91A). T1 without apical fascia, usually with bright orange-yellow basal fascia; T2 with bright orange-yellow apical fascia (Fig. 26A–C) ..... ***E. bifasciatus* Cresson**

\- Head with frontal area without protrusions (Fig. 91B). Metasomal terga with white to pale gray or pale yellow short appressed setae; IF with bright orange-yellow short appressed setae, THEN T1 with well-developed apical fascia (Figs 32A–C, 39A–C) ..... 3

3 (2) Axilla with free portion ~2/5 its entire medial length or longer (Figs 4D, 12D, 81D); IF borderline ($0.35< x <0.4$), THEN axilla with lateral margin relatively straight (Fig. 18D); IF borderline ($0.35< x <0.4$) and axilla with lateral margin arcuate, THEN axilla with free portion distinctly hooked (i.e., concave, not relatively straight along medial margin) (Figs 32D, 53D, 63D) ..... 4

\- Axilla with free portion clearly less than 2/5 its entire medial length. Axilla with lateral margin usually distinctly arcuate. Figs 8D, 16D, 24D, 39D, 49D, 55D, 71D,

73D, 77D, 79D, 83D) ..... 11

4 (3) Mesopleuron with punctures in ventrolateral half sparse (most i>1d), the interspaces shining (Fig. 92A)..... 5

- Mesopleuron with punctures in ventrolateral half dense (most i≤1d) or mesopleuron rugose with punctures ill-defined, the interspaces shining or dull due to surface microsculpture (Fig. 92B) ..... 7

5 (4) Metasomal terga with punctures large and deep (Fig. 93A). T2–T4 with fasciae complete and evenly broad (Fig. 65B) ..... ***E. lectus* Cresson (in part)**

- Metasomal terga with punctures minute and shallow (Fig. 93B). If fasciate, T2–T4 with fasciae conspicuously narrowed or interrupted medially (Fig. 63B) ..... 6

6 (5) Pronotal collar, axilla, mesoscutellum, and discs of T1 and T2 ferruginous. Metasomal terga with pale pubescence commonly reduced to discrete lateral patches. Fig. 53..... ***E. glabratus* Cresson**

- At least pronotal collar and metasomal terga entirely black. Metasomal terga fasciate. Fig. 63A–C..... ***E. lectoides* Robertson**

7 (4) Metanotum with distinct posteromedial depression (Fig. 94A). T2 fascia with lobe-like anterolateral extensions of tomentum (Fig. 18A–C) [west of Continental Divide]..... ***E. axillaris* sp. n.**

- Metanotum without depression (Fig. 94B). T2 fascia without lobe-like anterolateral extensions of tomentum (Figs 4A–C, 32A–C, 81A–C), although fascia may be broader laterally with sparser pale hairs basally (Fig. 12A–C) [east of Continental Divide]..... 8

8 (7) Head with preoccipital ridge joining hypostomal carina (approximately at 2/5 length of proboscidial fossa) (Fig. 95A). Mandible simple (assess only if mandible fully extended) (Fig. 3A)..... ***E. ainsliei* Crawford**

- Head with preoccipital ridge not joining hypostomal carina (Fig. 95B). Mandible with small, obtuse preapical tooth (assess only if mandible fully extended) (Fig. 3B, C) ..... 9

9 (8) Mesoscutum with paramedian band. Metasomal fasciae bright yellow to brownish orange and interrupted medially. Fig. 32B [Southeastern United States] ..... ..... ***E. carolinus*** **Mitchell**

- Mesoscutum largely obscured by pale tomentum in anterior half, tomentum densest anteromedially or evenly dense throughout mesoscutum. Metasomal fasciae off white to pale yellow and complete. Figs 12B, 81B [Great Plains and parts of American Southwest] ..... 10

10 (9) F2 of female less than 1.2 × as long as wide (Fig. 96A). T1 in dorsal view with longitudinal band more than half as wide as breadth of apical fascia (Fig. 12B) ..... ..... ***E. attenboroughi*** **sp. n.**

- F2 of female more than 1.2 × as long as wide (Fig. 96B). T1 in dorsal view with discal patch so wide that longitudinal band barely visible (its width less than half the breadth of apical fascia) (Fig. 81B) ..... ***E. rufulus*** **Cockerell**

11 (3) T1–T3 with apical fasciae distinctly interrupted medially, T4 with fascia interrupted or narrowed medially (Figs 8B, 39B, 49B, 55B, 77B). Axilla and mesoscutellum ferruginous (Figs 8D, 39D, 49D, 55D, 77D)..... 12

- T1–T3 with apical fasciae complete or only very narrowly interrupted medially, T4 with fascia complete (Figs 16B, 24B, 71B, 73B, 79B, 83B). Axilla and mesoscutellum color variable, may be entirely black (Fig. 16D) or partially to entirely ferruginous (Figs 24D, 71D, 73D, 79D, 83D) ..... 16

12 (11) T1 with basal fascia absent or reduced to pair of small patches of pale tomentum (Figs 39B, 77B). T5 with pseudopygidial area of female with apex more than twice as wide as medial length (Fig. 97A). T1 without longitudinal band (Figs 39A, C, 77A, C) ..... 13

- T1 with basal fascia well developed, complete or narrowly interrupted medially (Figs 8B, 49B, 55B). T5 with pseudopygidial area of female with apex less than twice as wide as medial length (Fig. 97B). T1 with (Figs 8C, 49C, 55A, C) or without (Figs 8A, 49A) longitudinal band ..... 14

13 (12) T1–T4 with apical fasciae brownish orange, at least medially (usually off white laterally) (Fig. 39A–C), those of T1 and T2 particularly well-developed. Mesopleuron commonly with punctures in ventrolateral half sparse (i≤2d), the interspaces shining or somewhat dull due to tessellate surface microsculpture (Fig. 92C) [adults active from late spring to early summer]..... ***E. deyrupi*** **sp. n.**

- T1–T4 with bands of pale pubescence rather uniformly off white, usually reduced to discrete lateral patches that peter out medially (Fig. 77A–C). Mesopleuron with punctures in ventrolateral half dense (most i<1d) (Fig. 92D) [adults active in autumn]..... ***E. packeri*** **sp. n.**

14 (12) Mesoscutum and metasomal terga with bands of pale gray to white short appressed setae. T1 with few exceptions ferruginous. Fig. 49A–C ..... ***E. floridensis*** **Mitchell**

- Mesoscutum and metasomal terga with bands of bright or pale yellow short appressed setae. T1 black. Figs 8A–C, 55A–C ..... 15

15 (14) Axilla with tip not extending as far back as posterior margin of mesoscutellum, mesoscutellum dark brown or black basally (Fig. 8D)..... ***E. andriyi*** **sp. n.**

- Axilla with tip extending as far back as or beyond posterior margin of mesoscutellum, axilla and mesoscutellum entirely red (Fig. 55D) ..... ..... ***E. howardi*** **Mitchell**

16 (11) Axilla with tip well short of band of pale tomentum along posterior margin of mesoscutellum (Fig. 16D), axilla and mesoscutellum entirely black. T2 fascia without anterolateral extensions of tomentum (Fig. 16A–C)..... ..... ***E. autumnalis*** **Robertson**

- Axilla with tip extending to or beyond band of pale tomentum along posterior margin of mesoscutellum (may be just short of band at apicomedial extent of mesoscutellum) (Figs 24D, 71D, 73D, 79D, 83D), axilla with few exceptions ferruginous to some degree. T2 fascia with (Figs 24A–C, 71A–C, 73A–C, 79A–C) or without (Fig. 83A, B) anterolateral extensions of tomentum..... 17

17 (16) Mesopleuron of male obscured by white tomentum only in upper half (although hypoepimeral area usually with sparser tomentum), with a large, sparsely hairy circle occupying much of ventrolateral half (Fig. 83C). T5 with pseudopygidial area of female with apex clearly more than twice as wide as medial length (~2.5–3 × the medial length) (Fig. 97C). Axilla with tip extending to or beyond band of pale tomentum along posterior margin of mesoscutellum, mesoscutellum entirely black to entirely ferruginous (Fig. 83D) .....***E. scutellaris*** **Say**

- Mesopleuron of male (excluding hypoepimeral area) entirely obscured by white tomentum (Figs 24C, 71C, 73C, 79C). T5 with pseudopygidial area of female with apex about twice as wide as medial length or less (clearly <2.5 × the medial length) (Fig. 97D, E). Axilla with tip at most extending to band of pale tomentum along posterior margin of mesoscutellum, mesoscutellum entirely black (Figs 24D, 71D, 73D, 79D)..... 18

18 (17) Flagellum, except sometimes F1, and metasomal sterna (excluding apical margins) brown or black, clearly not the same reddish-orange color as legs from tibiae to tarsi (Fig. 98A). T1 with longitudinal extent of discal patch no less (and usually greater) than breadth of apical fascia (Fig. 79B). T1–T3 with apical fasciae removed from apical margin, commonly narrowed or narrowly interrupted medially (Fig. 79A–C) [southern Canada and much of contiguous U.S., east of the Rocky Mountains].....***E. pusillus*** **Cresson**

- Metasomal sterna reddish brown or reddish orange (Fig. 98B); IF brown or black, THEN rarely entire flagellum also brown or black. T1 with longitudinal extent of discal patch variable, but may be less than breadth of apical fascia (Figs 71B, 73B). T1–T3 with apical fasciae on apical margin and evenly broad (Figs 71A–C, 73A–

C) or as above (Fig. 24A–C) [U.S., Great Plains to West Coast] ..... 19

19 (18) T2 and T3 (for female) or T2–T4 (for male) with fasciae removed from apical margin, commonly narrowed or narrowly interrupted medially (Fig. 24A–C). T5 with pseudopygidial area of female with apex at least twice as wide as medial length (Fig. 97D). T1 with longitudinal extent of discal patch greater than breadth of apical fascia, at least medially (Fig. 24B) ..... ***E. basili* sp. n.**

- T2–T4 with fasciae on or very little removed from apical margin, more or less evenly broad (Figs 71A–C, 73A–C). T5 with pseudopygidial area of female with apex commonly less and no more than twice as wide as medial length (Fig. 97E). T1 with longitudinal extent of discal patch variable, but commonly less than breadth of apical fascia (Figs 71B, 73B) ..... 20

20 (19) Metasomal terga (excluding brown translucent apical margins) black (Figs 71B, 99A). Mesoscutum obscured by pale tomentum (Fig. 71B, C).... ***E. nebulosus* sp. n.**

- At least T1 with integument beneath apical fascia ferruginous (Fig. 99B), T1 basally and other terga sometimes partially to entirely ferruginous as well (Fig. 73B). Mesoscutum with well-defined paramedian band (Fig. 73B) or obscured by pale tomentum ..... ***E. novomexicanus* Cockerell**

21 (1) Head with vertexal area with two pairs of shiny (usually impunctate) protrusions (Fig. 91C). T2 fascia with two pairs of anterolateral extensions of tomentum (Figs 1, 34A–C, 41A, C)..... 22

- Head with vertexal area without protrusions (Fig. 91D). T2 fascia with single pair of anterolateral extensions of tomentum (Figs 6A–C, 10A–C, 14A–C, 20A, C, 28A–C, 43A–C, 51A–C, 59A–C, 61A–C, 65A–C, 69A–C, 75A–C, 87A–C) or without (Figs 22A–C, 30A–C, 36A–C, 38, 45A–C, 47A–C, 57A–C, 67A–C, 85A–C, 89A–C) anterolateral extensions of tomentum ..... 23

22 (21) Mesopleuron with punctures in ventrolateral half sparse (most i>1d), the interspaces shining (Fig. 92I) [Southwestern United States] ..... ..... ***E. chamaesarachae* sp. n.**

- Mesopleuron with punctures in ventrolateral half dense (most i≤1d) (Fig. 92J) [Coastal and South Texas]..... ***E. diadematus* sp. n.**

23 (21) Axilla with free portion about 2/5 its medial length or longer and distinctly hooked (i.e., concave, not relatively straight along medial margin) (minimum free extent shown in Fig. 65D) (see also Figs 43D, 51D, 57D, 59D, 89D). T5 with pseudopygidial area of female distinctly campanulate, with apex less than twice as wide as medial length (Fig. 97F–H) ..... 24

- Axilla with free portion less than 2/5 its entire medial length (usually ≤ 1/3) and relatively straight along medial margin (maximum free extent shown in Fig. 75D) (see also Figs 6D, 10D, 14D, 20D, 22D, 28D, 30D, 36D, 45D, 47D, 61D, 67D, 69D, 85D, 87D). T5 with pseudopygidial area of female lunate (Fig. 97I) or present as very narrow transverse band (Fig. 61B), with apex at least twice as wide as medial length ..... 29

24 (23) Axilla and mesoscutellum entirely ferruginous. T1 and T2 ferruginous. Fig. 89 ..... ..... ***E. zonatus* Smith**

- Axilla and mesoscutellum at least partially dark brown or black. T1 and T2 black. Figs 43, 51, 57, 59, 65 ..... 25

25 (24) Mesopleuron very coarsely and densely rugose-punctate AND punctures of varying size, few if any interspaces as large as puncture diameters (Fig. 92E) ..... ..... ***E. erigeronis* Mitchell**

- Mesopleuron with larger interspaces (i≈1d) typically more numerous (Fig. 92A, F); IF most interspaces small (i<1d), THEN mesopleuron more finely and minutely punctate AND punctures of similar size throughout mesopleuron (Fig. 92G)..... 26

26 (25) Metasomal terga with punctures large and deep (Fig. 93A). T2–T4 with fasciae complete and evenly broad (Fig. 65A–C) ..... ***E. lectus*** **Cresson (in part)**

Metasomal terga with punctures minute and shallow (Fig. 93C). T2–T4 with fasciae commonly narrowed or interrupted medially (Figs 51B, 57B, 59B) ..... 27

27 (26) Mandible with blunt, obtuse preapical tooth (Fig. 3D). F2 of female less than 1.2 × as long as wide (Fig. 96C). Legs with brown or black more extensive than reddish orange, at least from metacoxa to metatibia (Fig. 51A, C). S4 and S5 of male with long curved coppery to silvery subapical hairs, many extending beyond apex of sternum by 1 MOD or more (Fig. 51C). T5 of female with two large patches of pale tomentum parallel to and contacting pseudopygidial area nearly throughout its length (Fig. 97F)..... ***E. gibbsi*** **sp. n.**

- Mandible simple (Fig. 3E). F2 of female more than 1.2 × as long as wide (Fig. 96D). Legs extensively reddish orange (Fig. 57A, C) or brown or black (Fig. 59A, C); IF male and legs with brown or black more extensive than reddish orange from metacoxa to metatibia, THEN S4 and S5 with short straight subapical hairs, extending little (clearly by <1 MOD) if at all beyond apex of sternum (Fig. 100B). T5 of female with two large patches of pale tomentum lateral to and separate from pseudopygidial area, or contacting pseudopygidial area at apex, diverging from it basally (Fig. 97G)..... 28

28 (27) Pronotal lobe and legs more extensively reddish orange than brown or black, metatibia with anterior surface same reddish orange color as metatarsus (Fig. 57A, C). Pronotal collar, mesoscutum, and metasomal terga with bands of gray to pale yellow short appressed setae (Fig. 57). S4 and S5 of male with long curved coppery to silvery subapical hairs, many extending beyond apex of sternum by 1 MOD or more (Fig. 100A)..... ***E. ilicis*** **Mitchell**

- Pronotal lobe black to partially or entirely reddish orange. Legs usually darker (with brown or black more extensive than reddish orange), at least from metacoxa to metatibia (Fig. 59A, C). Pronotal collar, mesoscutum, and metasomal terga with bands of gray short appressed setae (Fig. 59). S4 and S5 of male with short straight

subapical hairs, extending little (clearly by <1 MOD) if at all beyond apex of sternum (Fig. 100B) ..... ***E. inornatus* sp. n.**

29 (23) Mesoscutum with anteromedial patch of bright or pale yellow tomentum, usually chevron-, horseshoe-, or V-shaped and narrowed anterolaterally (Figs 30B, 36B, 38, 45B) but sometimes semicircular (Fig. 85B) ..... 30

- Mesoscutum with gray or bright to pale yellow paramedian band (usually parallel and not joined except sometimes posteriorly) (Figs 6B, 10B, 14B, 20B, 28B, 47B, 61B, 67B, 69B, 75B, 87B) or largely obscured by pale tomentum (Fig. 101B); IF joined posteriorly (i.e., U- or V-shaped), THEN not distinctly narrowed anterolaterally (Fig. 101A) ..... 33

30 (29) Propodeum with posterior surface highly polished and (except along lateral margin) hairless (Fig. 102A). T1 with broad, transverse off-white basal fascia, discal patch greatly reduced or absent; T1–T4 with complete bright yellow apical fasciae, terga otherwise covered in brown (and laterally sometimes off-white) tomentum (Fig. 85A–C) ..... ***E. splendidus* sp. n.**

- Propodeum with posterior surface dull due to surface microsculpture and with long erect hairs submedially (Fig. 102B). T1 with median black or nearly black discal patch surrounded by pale tomentum; T1–T4 with complete or medially-interrupted pale yellow apical fasciae, terga otherwise covered in black or nearly black tomentum (Figs 30A–C, 36A–C, 38B, 45A–C) ..... 31

31 (30) T1 discal patch triangular or semicircular (with lateral sides straight or convex), basal fascia fully continuous with longitudinal band AND discal patch more elongate, its medial longitudinal extent (measured as if apical fascia were complete) more than 1/3 the lateral extent. Fig. 30B ..... ***E. canadensis* Mitchell**

- T1 discal patch quadrangular (basal and apical fasciae subparallel and separated by longitudinal band) (Figs 36B, 45B) or diamond-shaped (Fig. 38) with basal and apical fasciae broadly joined laterally; IF discal patch almost semicircular, THEN shorter, its medial longitudinal extent (measured as if apical fascia were complete)

at most 1/3 the lateral extent..... 32

32 (31) T2–T4 with fasciae broadened before becoming narrowed or separated into rounded lobes medially, and usually narrowed before becoming somewhat broader laterally (Figs 36B, 38)..... ***E. compactus* Cresson**

- T2–T4 with fasciae not broadened into rounded lobes medially, and somewhat broader laterally and complete or tapering until separated medially (Fig. 45B)..... .....***E. ferrarii* sp. n.**

33 (29) T1 with median triangular or semicircular discal patch (basal fascia conspicuously arched, apical fascia straight) AND longitudinal band at least half as wide as breadth of apical fascia in dorsal view (Fig. 47B).....***E. flavofasciatus* Smith**

- T1 not as above; IF discal patch triangular, THEN so wide that longitudinal band barely visible in dorsal view (its width less than half the breadth of apical fascia) (Fig. 61B) ..... 34

34 (33) T2–T4 with apical fasciae complete, evenly broad (Figs 14B, 28B, 67B) ..... 35

- T1 and T2 with apical fasciae broken or at least greatly narrowed medially, those of T3 and T4 broken or complete (Figs 6B, 10B, 20B, 22B, 61B, 69B, 75B, 87B) ... 37

35 (34) Fore wing with two submarginal cells, apically dusky in female, hyaline throughout in male (Fig. 67A, C). Axilla with free portion commonly less than 1/4 as long as its entire medial length (Fig. 67D). Mesopleuron almost entirely obscured by tomentum, at least in male (Fig. 67C). Axilla and mesoscutellum black (Fig. 67)..... .....***E. mesillae* (Cockerell)**

- Fore wing with three submarginal cells, subhyaline, apically dusky in both sexes (Fig. 14A, 28A). Axilla with free portion at least 1/4 as long as its entire medial length (Figs 14D, 28D). Mesopleuron obscured by tomentum only in upper half, with a large, sparsely hairy circle occupying much of ventrolateral half (Figs 14A, C, 28A, C). At least axilla ferruginous in part (Figs 14A, B, D, 28B, D)..... 36

36 (35) Frontal carina strongly convex, such that supraclypeal area distinctly protuberant in lateral view (Fig. 103A). Pygidial plate of male narrow, with medial length ~1.5 × basal width (Fig. 2A). T2 fascia with anterolateral extensions of tomentum strongly convergent basally (angle from apical fascia <45°) (Fig. 14B). ***E. australis* Mitchell**

\- Frontal carina weakly convex, such that supraclypeal area barely protuberant in lateral view (Fig. 103B). Pygidial plate of male broad, with medial length ≈ basal width (Fig. 2B). T2 fascia with anterolateral extensions of tomentum not so strongly convergent basally (angle from apical fascia 45° to 90°) (Fig. 28B)..... .....***E. brumleyi* sp. n.**

37 (34) Mesopleuron with punctures in ventrolateral half well separated (i>1d), usually upper half more densely punctate than ventrolateral half (Fig. 92H). Axilla and mesoscutellum (except sometimes in *E. interruptus*) ferruginous (Figs 61, 87). T1 with discal patch variable; IF forming rounded triangle with lateral sides concave (Fig. 61B), THEN mesosomal features may exhibit alternative states (see below) 38

\- Mesopleuron with most interspaces between punctures small (i≤1d) (Fig. 92K) or mesopleuron rugose, with punctures ill-defined (Fig. 92L). Axilla (except sometimes the tip) and mesoscutellum black (Figs 6, 10, 20, 22, 69, 75). T1 with discal patch quadrangular (Figs 6B, 10B, 20B, 22B, 69B, 75B) ..... 39

38 (37) Metanotum with blunt median process, usually covered in pale tomentum but visible nonetheless (Fig. 61D). T1 with discal patch forming rounded triangle with lateral sides concave (Fig. 61B) .....***E. interruptus* Robertson**

\- Metanotum without process (Fig. 87D). T1 with discal patch trapezoidal, sometimes almost semicircular, with lateral sides not distinctly concave (Fig. 87B) .....***E. tessieris* sp. n.**

39 (37) F2 of female at most 1.1 × as long as wide (Fig. 96E). Axilla with free portion at most 1/4 as long as its entire medial length (Figs 6D, 10D, 22D). T2 fascia with (Figs 6A–C, 10A–C) or without (Fig. 22A–C) anterolateral extensions of tomentum ..... 40

- F2 of female at least 1.2 × as long as wide (Fig. 96F). Axilla with free portion more than 1/4 as long as its entire medial length (Figs 20D, 69D, 75D). T2 fascia with anterolateral extensions of tomentum (Figs 20A, C, 69A–C, 75A–C) ..... 42

40 (39) Legs extensively reddish orange, at least from tibiae to tarsi (sometimes trochanters and femora as well), pronotal lobe reddish orange (Fig. 22A–C). T3 and T4 with fasciae complete or interrupted but not reduced to separated circular patches of pale tomentum (Fig. 22B) .....***E. barberiellus*** **Cockerell**

- Legs brown or black, pronotal lobe black to partially or entirely reddish orange (Figs 6A–C, 10A–C). T3 and T4 with fasciae complete (Fig. 6B) or broken medially and/or laterally, and may be reduced to widely separated circular patches of pale tomentum (Fig. 10B) ..... 41

41 (40) Mesopleuron (Fig. 92K) and tegula with many punctures widely separated (i=1d). Pronotal lobe dark brown to black (Fig. 6A, C). T3 and T4 with fasciae complete (Fig. 6B) or broken medially and/or laterally (Fig. 6A, C), rarely into separated oval patches [widespread throughout North America]..... ***E. americanus*** **(Cresson)**

- Mesopleuron (Fig. 92L) and tegula with punctures very dense (most i<1d). Pronotal lobe black to partially or entirely reddish orange (Fig. 10A, C). T3 and T4 with fasciae broken or at least greatly narrowed laterally, as well as medially into separated or narrowly connected oval patches (Fig. 10B) [California and possibly surrounding states] .....***E. asperatus*** **Cockerell**

42 (39) T3 and T4 with fasciae broken or at least narrowed laterally, as well as medially. Pronotal lobe reddish orange. Fig. 75A–C ..... ***E. olympiellus*** **Cockerell**

- T3 and T4 with fasciae not broken laterally, and complete or narrowly interrupted medially (Figs 20A–C, 69A–C). Pronotal lobe black (Figs 20A–C, 69C) to partially or entirely reddish orange (Fig. 69A) ..... 43

43 (42) Integument entirely dark brown or black AND mesoscutum and metasomal terga with bands of gray short appressed setae (Fig. 20) [Mid-Atlantic and Southeastern United States] .....***E. banksi* (Cockerell)**

- Integument dark brown or black to partially or entirely ferruginous on labrum, antenna, pronotal lobe, and legs, except foreleg, from trochanters to tarsi. Mesoscutum and metasomal terga with bands of off-white to pale yellow short appressed setae. Fig. 69 [widespread throughout North America] ..... .....***E. minimus* (Robertson)**

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**Figures**

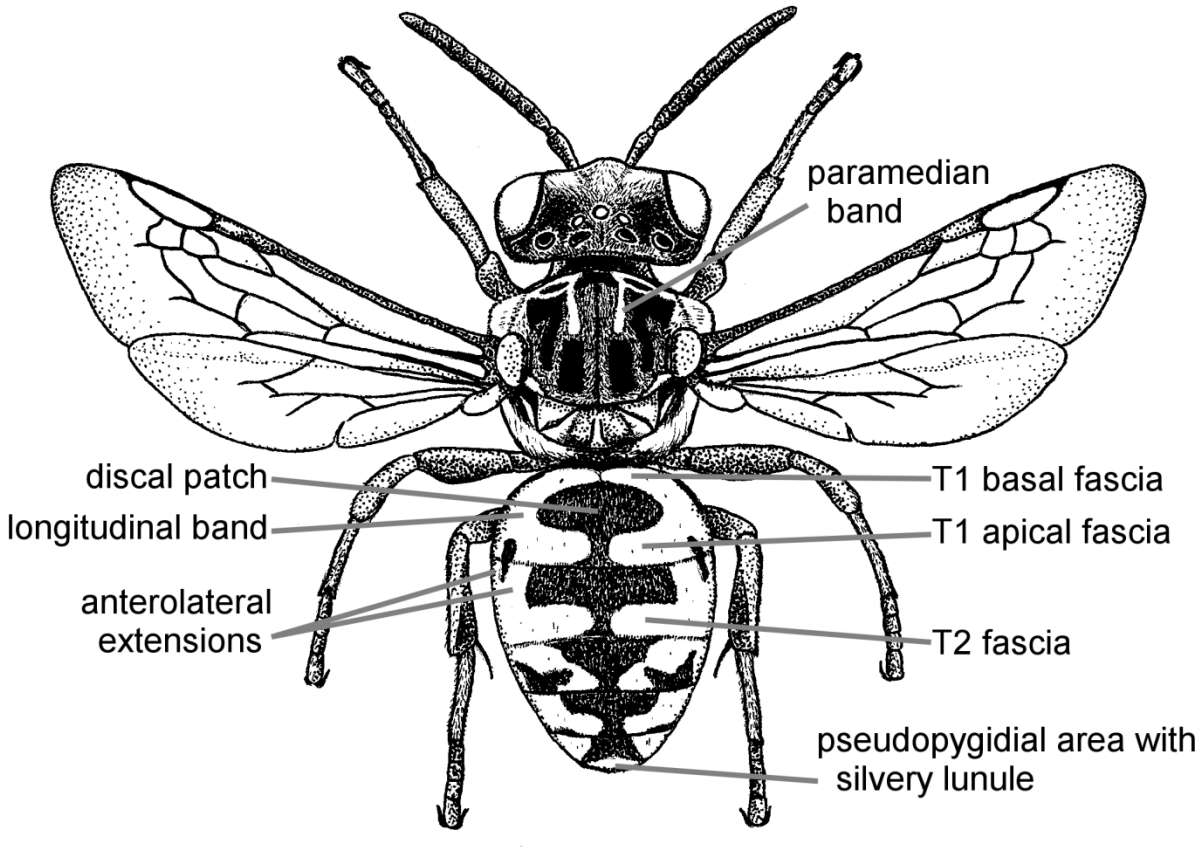


**Figure 1.** Female *E. chamaesarachae* sp. n. illustrating mesosomal and metasomal bands of tomentum commonly present in North American Epeolini.

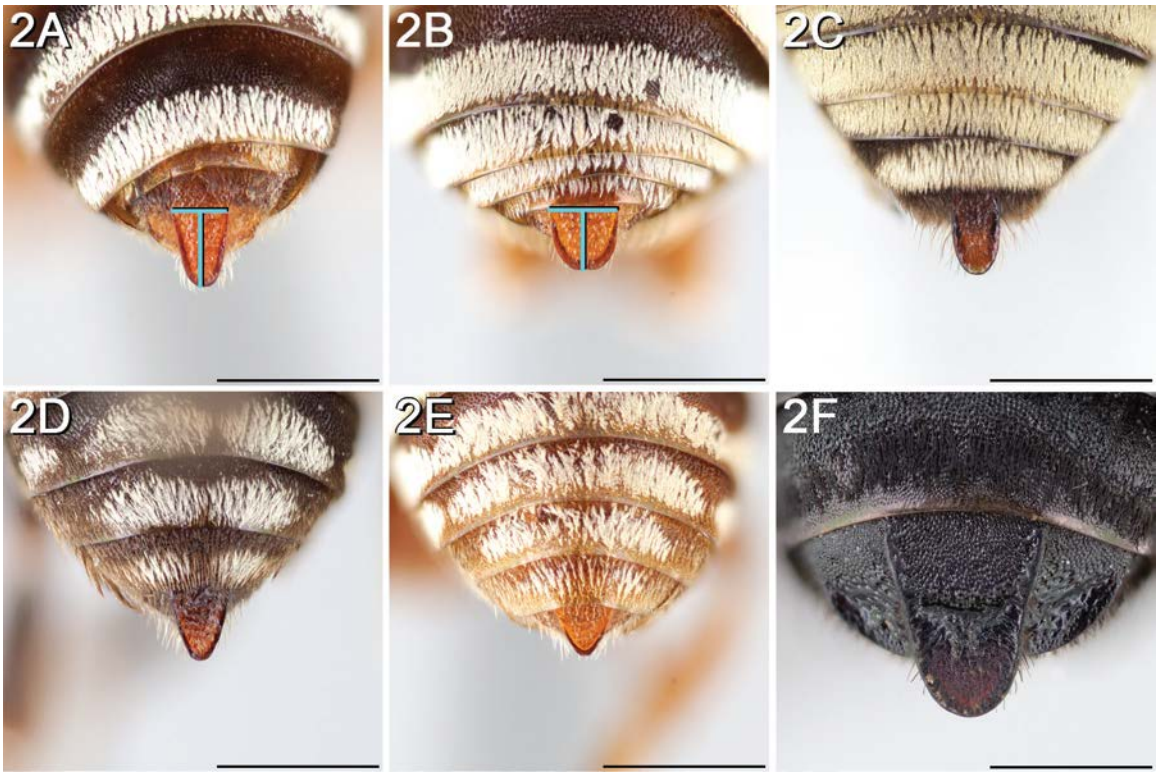


**Figure 2.** Pygidial plate (in dorsal view) of male **A** *E. australis* (longer than wide and apically narrowed), **B** *E. brumleyi* paratype (nearly as long as wide and apically rounded), **C** *E. flavofasciatus* (longer than wide, with the lateral margins parallel), **D** *E. asperatus* (longer than wide and apically narrowed), **E** *E. barberiellus* (somewhat longer than wide and apically narrowed), and **F** *T. concavus* (longer than wide, with the lateral margins somewhat concave). Scale bars 1 mm.

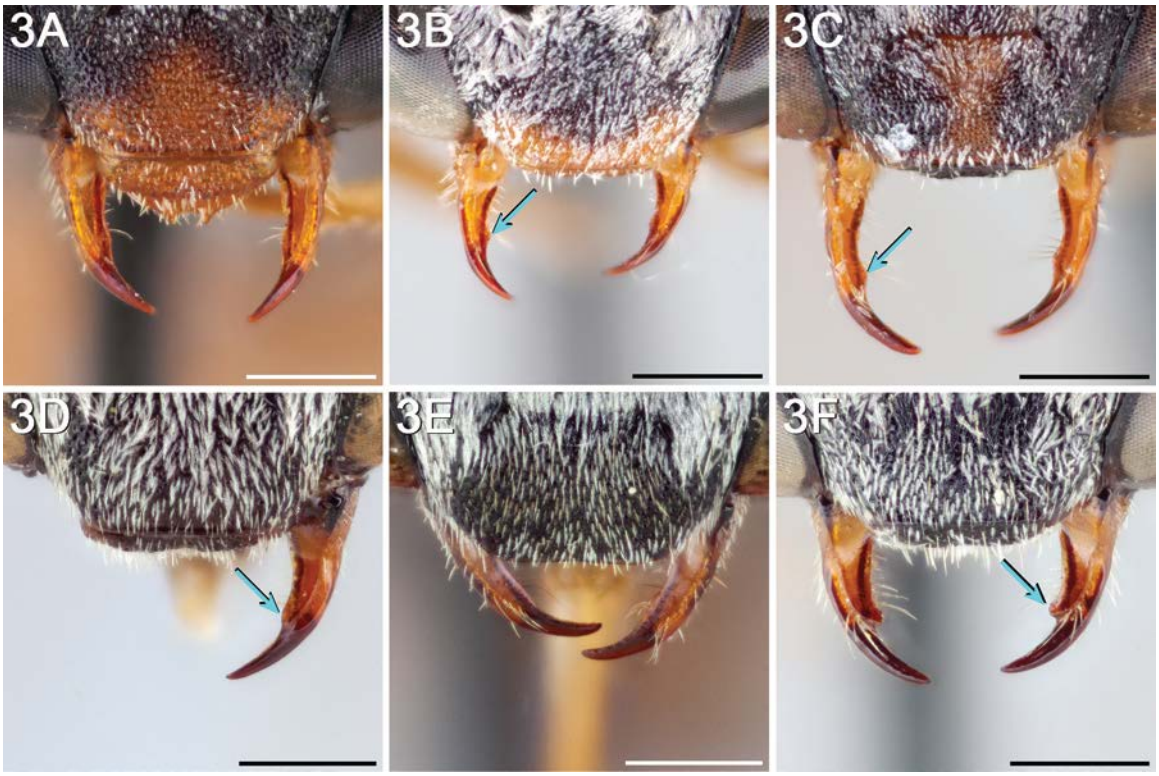


**Figure 3.** Mandible (in frontal view) of female **A** *E. ainsliei* without a preapical angulation or tooth, **B** *E. attenboroughi* holotype with an inconspicuous, obtuse preapical tooth, **C** *E. carolinus* with an inconspicuous, obtuse preapical tooth, **D** *E. gibbsi* paratype with an obtuse angle appearing like a tooth, **E** *E. vernalis* holotype (herein synonymized under *E. ilicis*) without a preapical angulation or tooth, and **F** *E. compactus* with a distinct preapical tooth with sides forming a right triangle. Scale bars 0.5 mm.

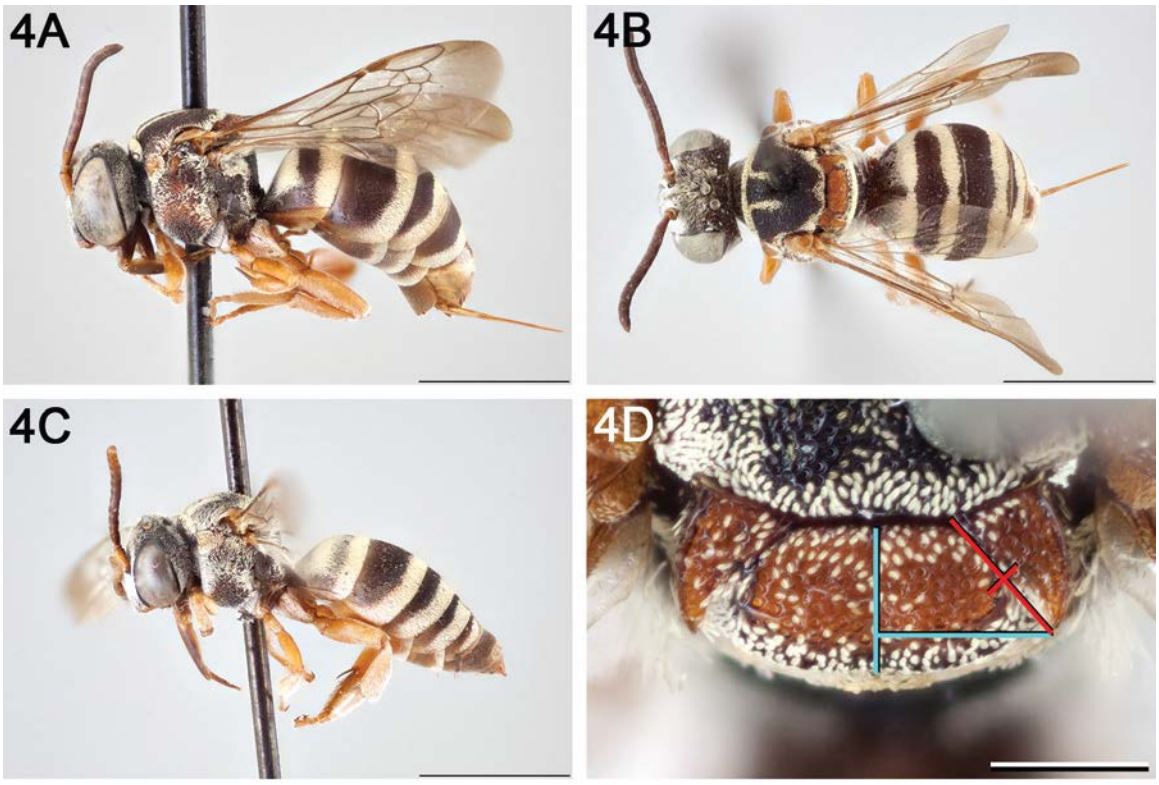


**Figure 4.** *Epeolus ainsliei* **A** female, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 5.** Approximate geographic range of *E. ainsliei* (orange) based on occurrence records known to the author (yellow circles).

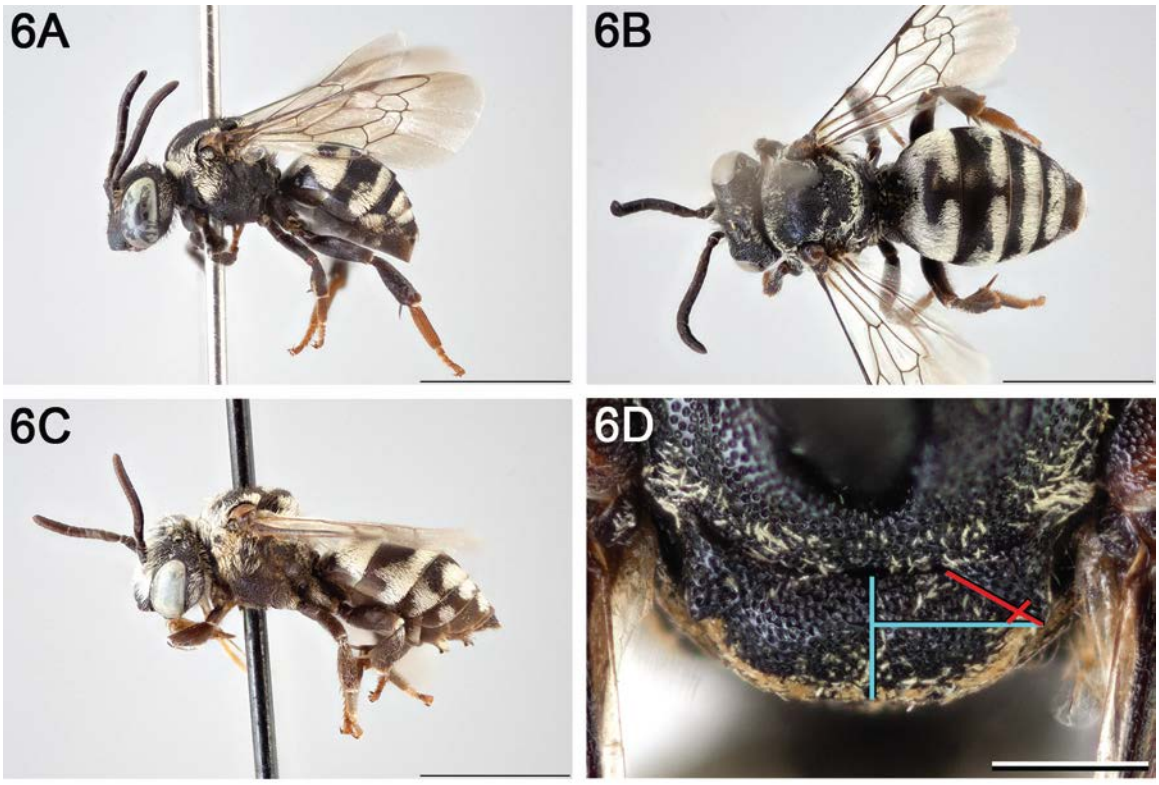


**Figure 6.** *Epeolus americanus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

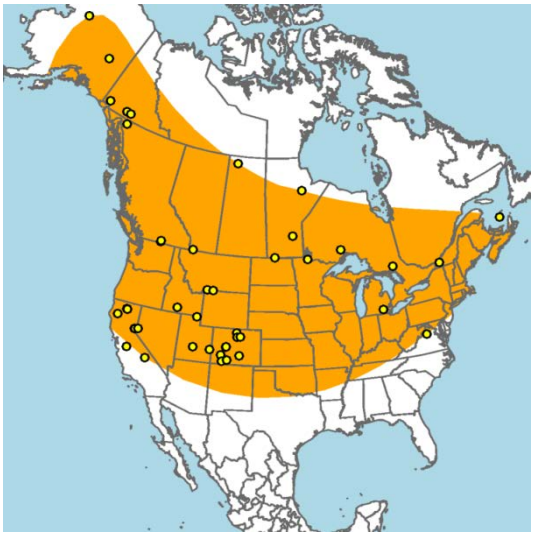

**Figure 7.** Approximate geographic range of *E. americanus* (orange) based on occurrence records known to the author (yellow circles).

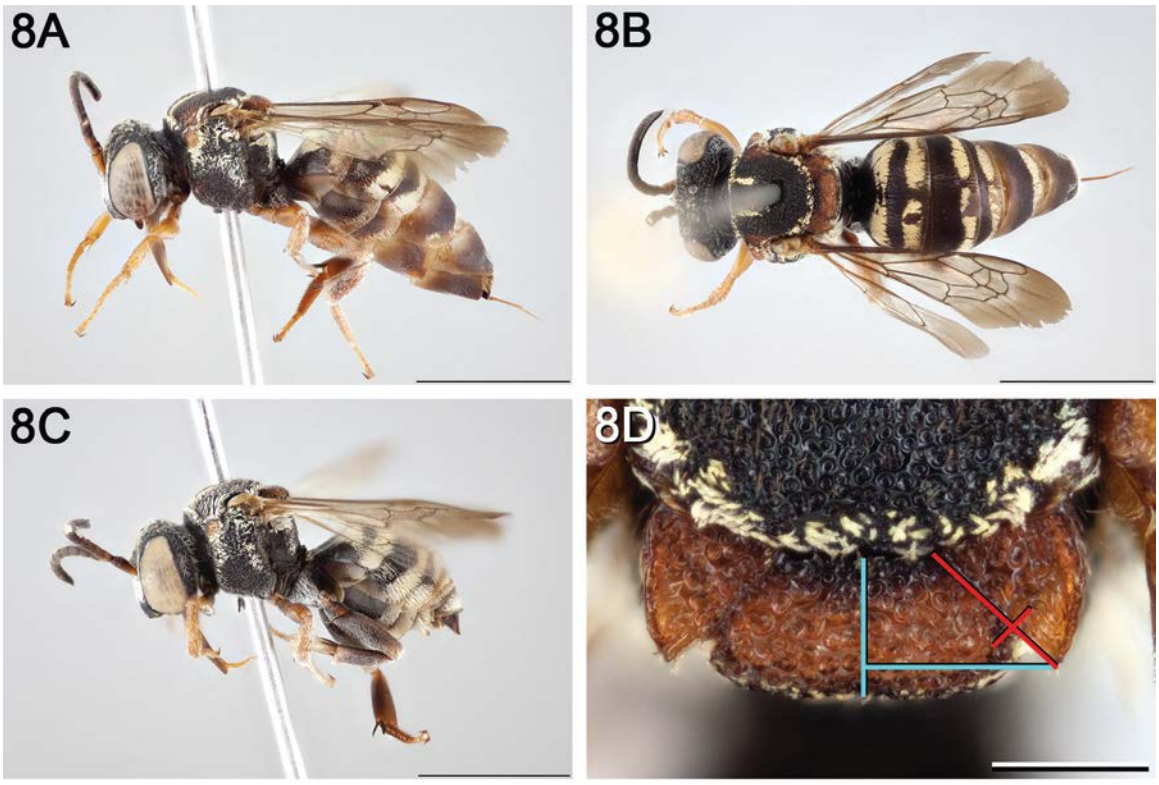


**Figure 8.** *Epeolus andriyi* **A** female holotype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male allotype, lateral habitus (scale bar 3 mm), and **D** female holotype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 9.** Occurrence record of *E. andriyi* known to the author (yellow circle).

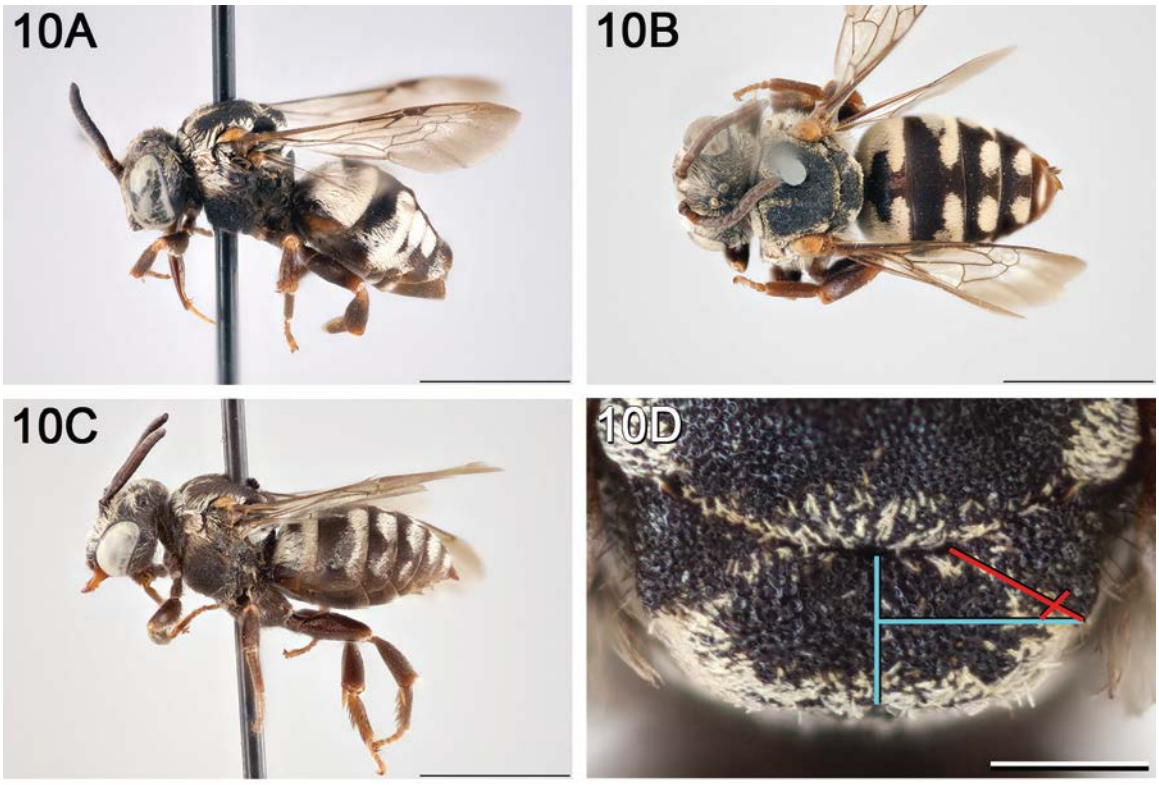


**Figure 10.** *Epeolus asperatus* **A** female, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 11.** Approximate geographic range of *E. asperatus* (orange) based on occurrence records known to the author (yellow circles).


**Figure 12.** *Epeolus attenboroughi* **A** female holotype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male allotype, lateral habitus (scale bar 3 mm), and **D** female holotype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 13.** Occurrence records of *E. attenboroughi* known to the author (yellow circles).


**Figure 14.** *Epeolus australis* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 15.** Approximate geographic range of *E. australis* (orange) based on occurrence records known to the author (yellow circles).

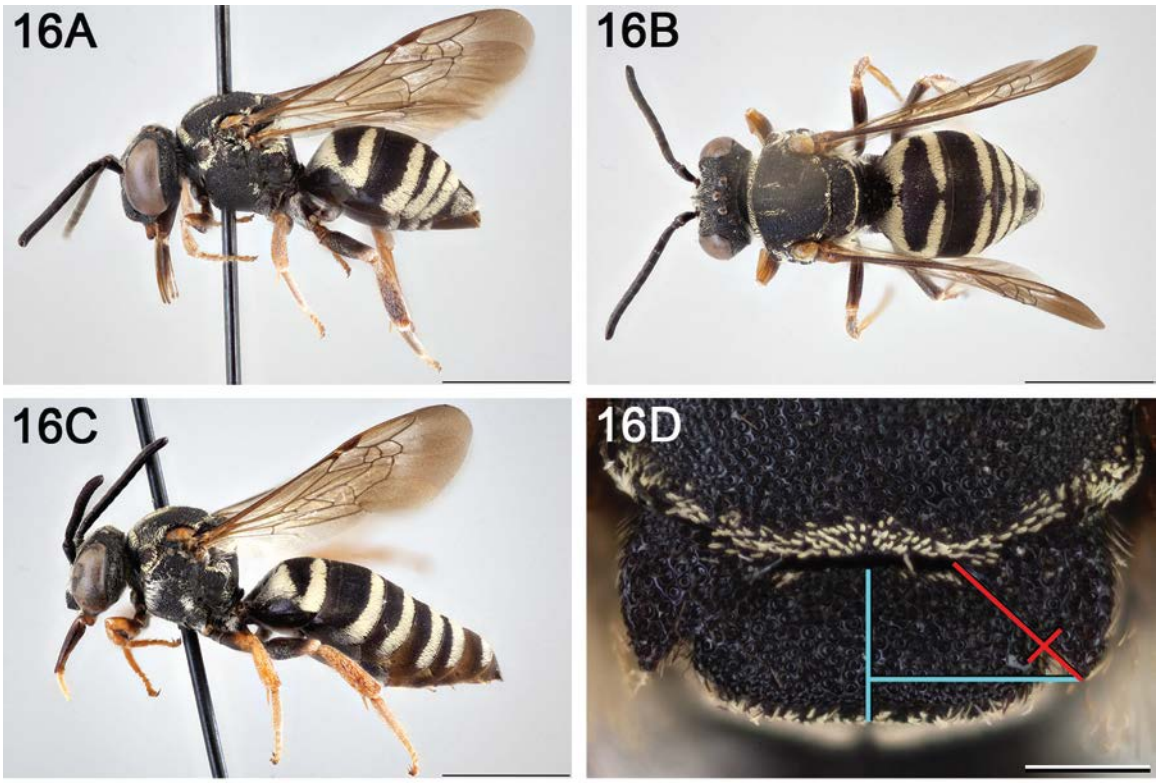


**Figure 16.** *Epeolus autumnalis* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 17.** Approximate geographic range of *E. autumnalis* (orange) based on occurrence records known to the author (yellow circles).

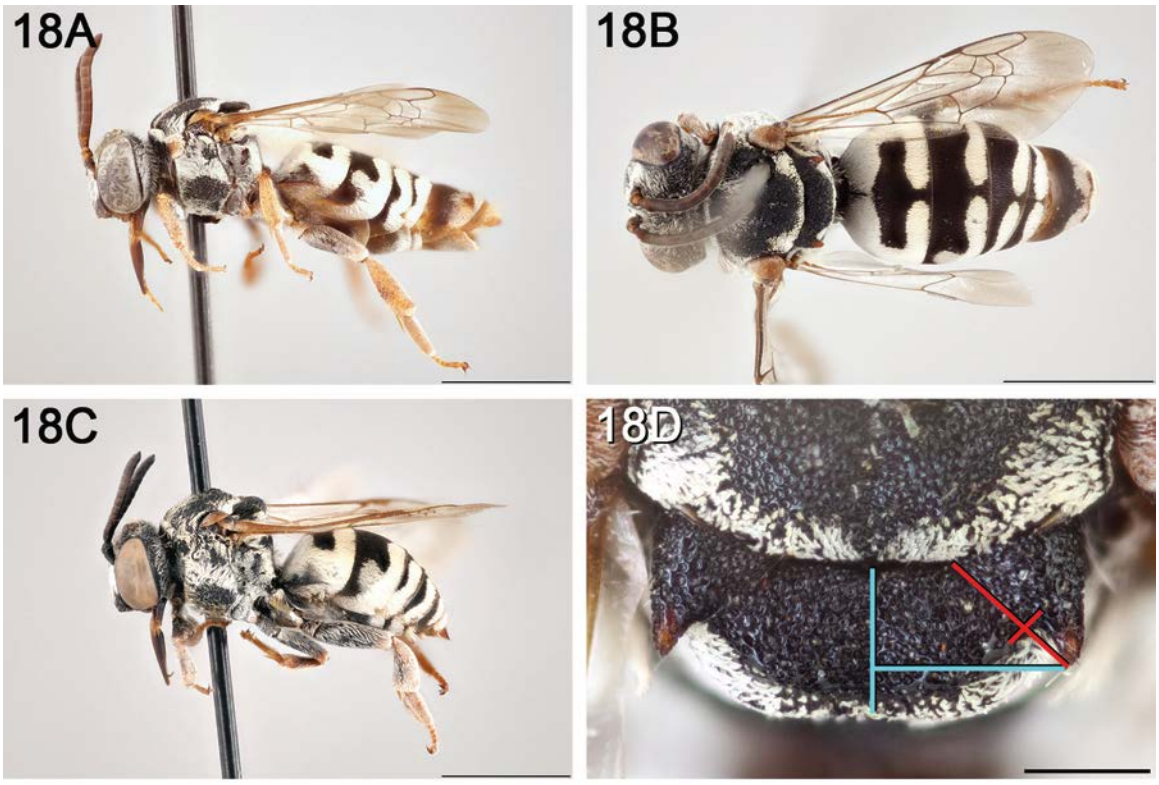


**Figure 18.** *Epeolus axillaris* **A** female paratype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male allotype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

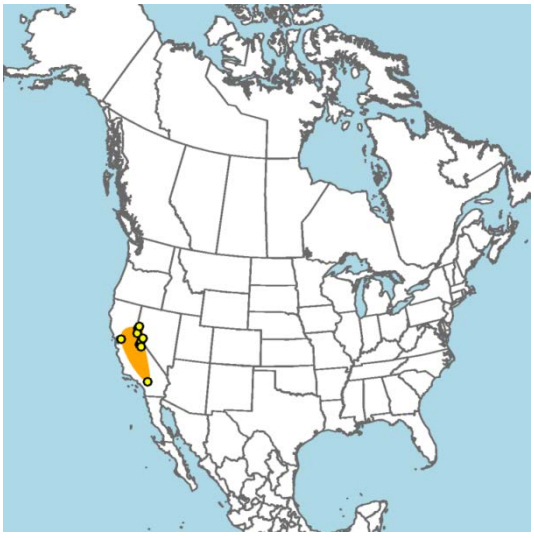

**Figure 19.** Approximate geographic range of *E. axillaris* (orange) based on occurrence records known to the author (yellow circles).

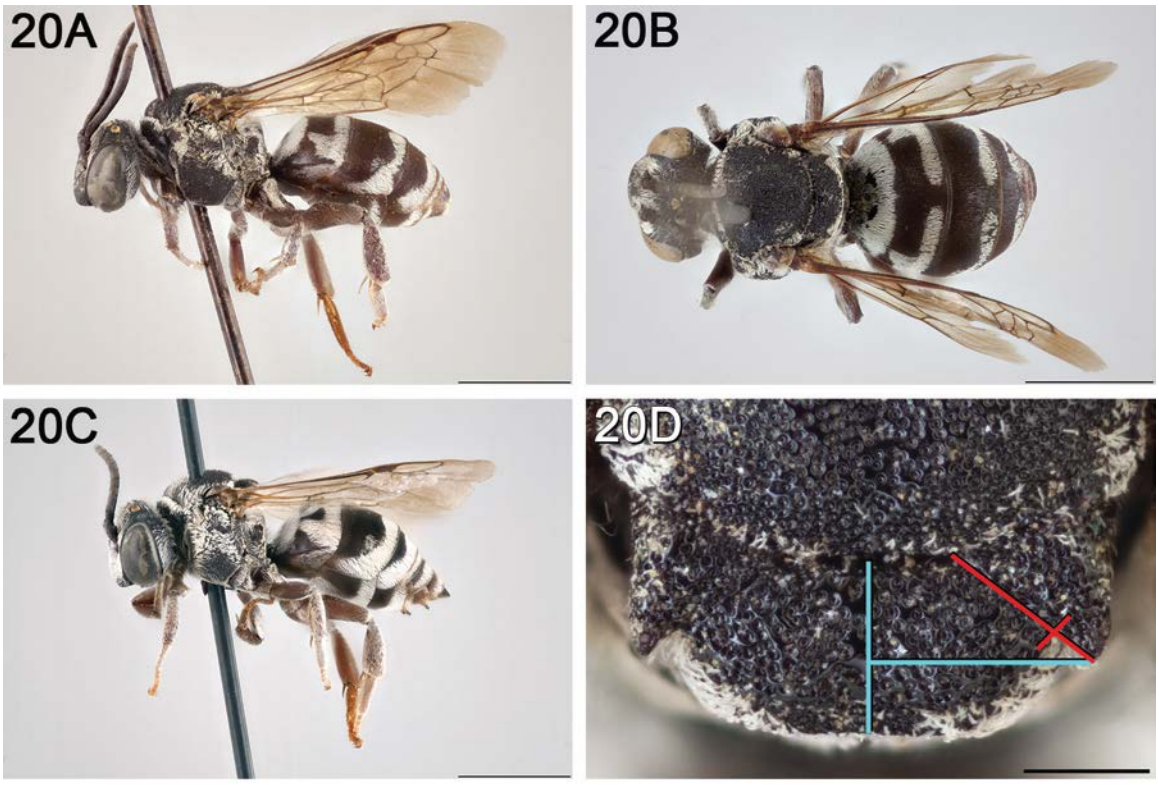


**Figure 20.** *Epeolus banksi* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 21.** Occurrence records of *E. banksi* known to the author (yellow circles).


**Figure 22.** *Epeolus barberiellus* **A** female, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female holotype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

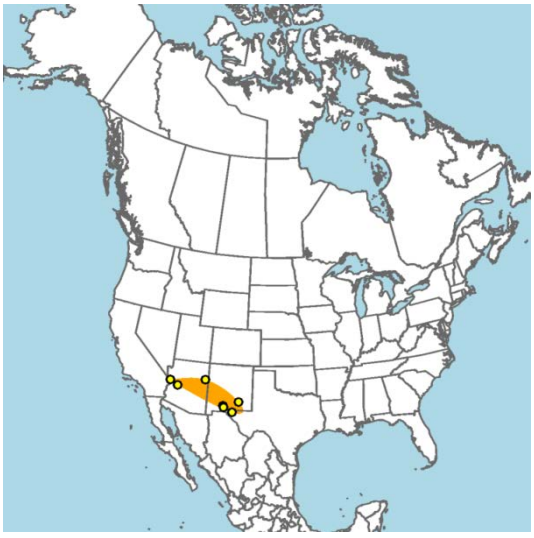

**Figure 23.** Approximate geographic range of *E. barberiellus* (orange) based on occurrence records known to the author (yellow circles).

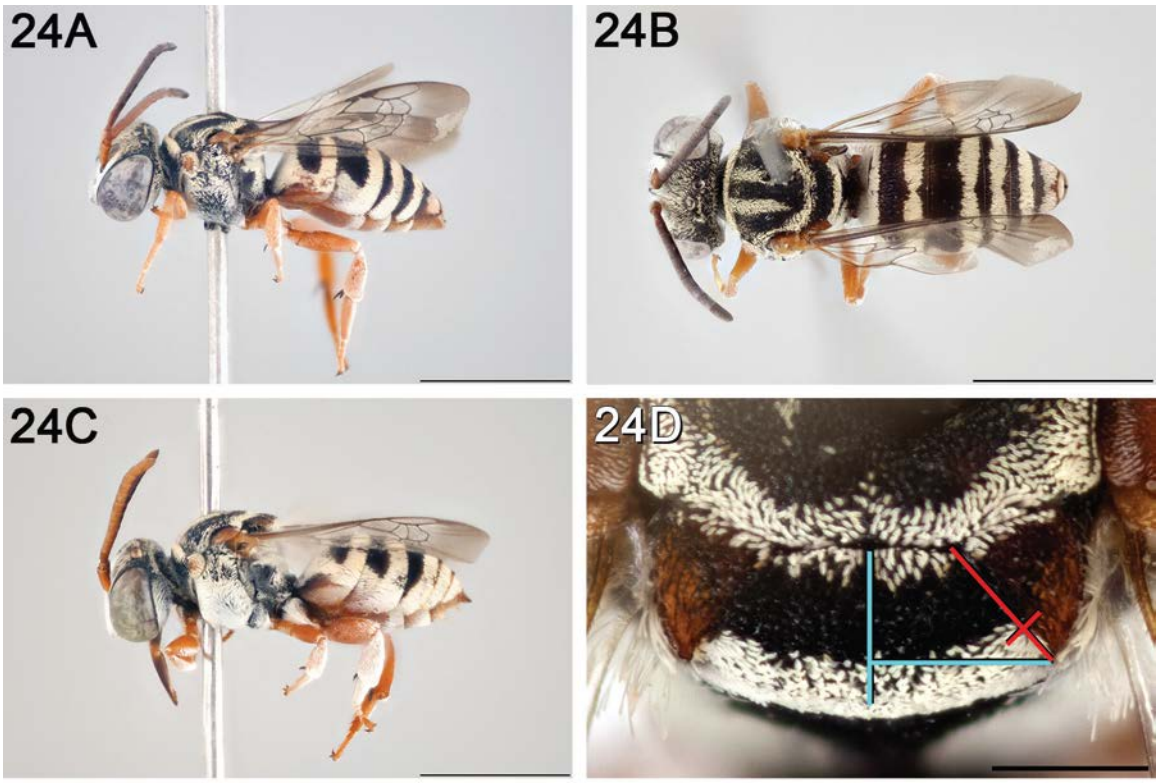


**Figure 24.** *Epeolus basili* **A** female holotype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male allotype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 25.** Approximate geographic range of *E. basili* (orange) based on occurrence records known to the author (yellow circles).

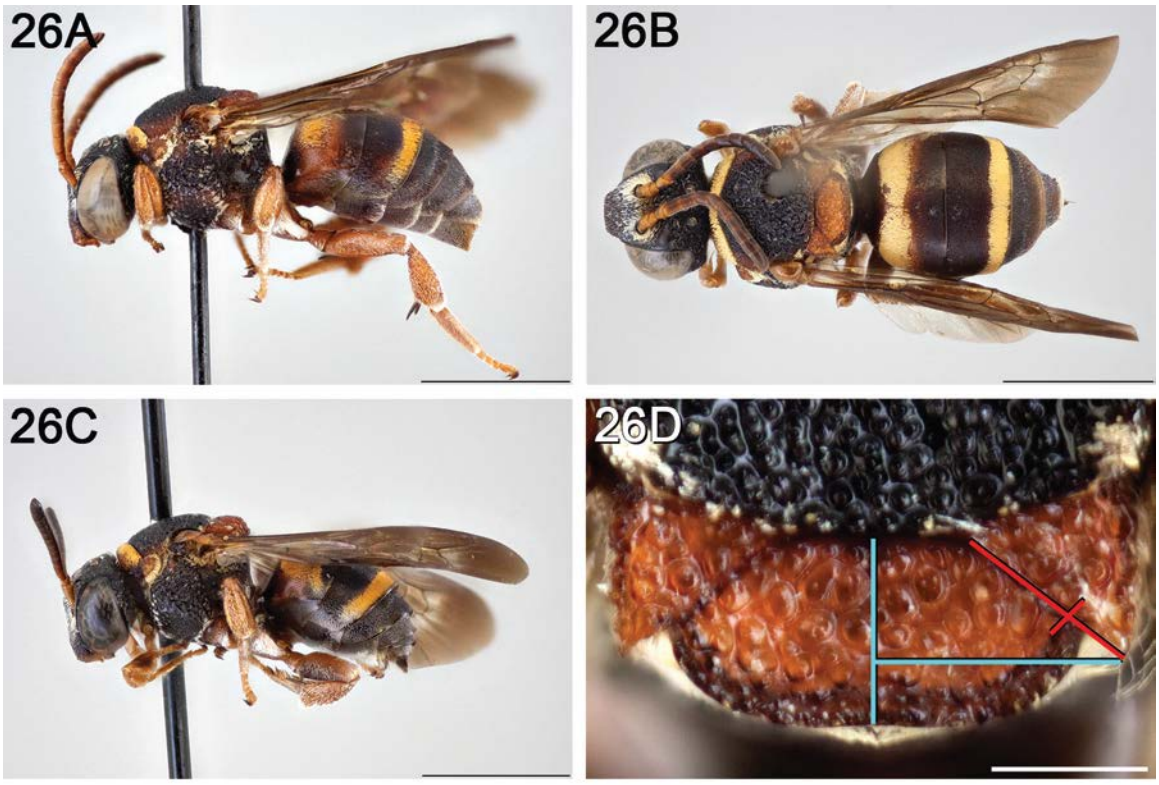


**Figure 26.** *Epeolus bifasciatus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

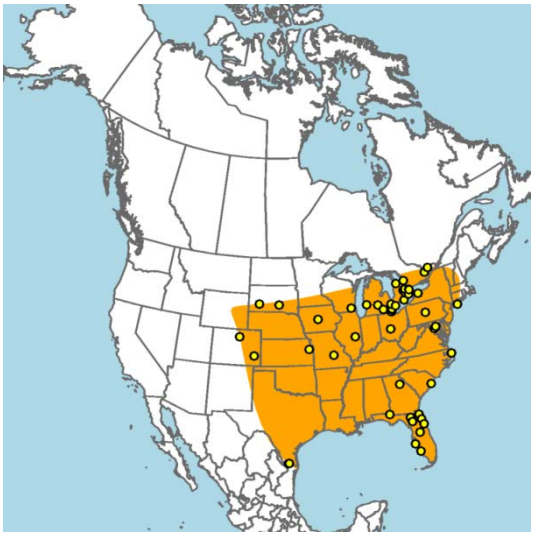

**Figure 27.** Approximate geographic range of *E. bifasciatus* (orange) based on occurrence records known to the author (yellow circles).

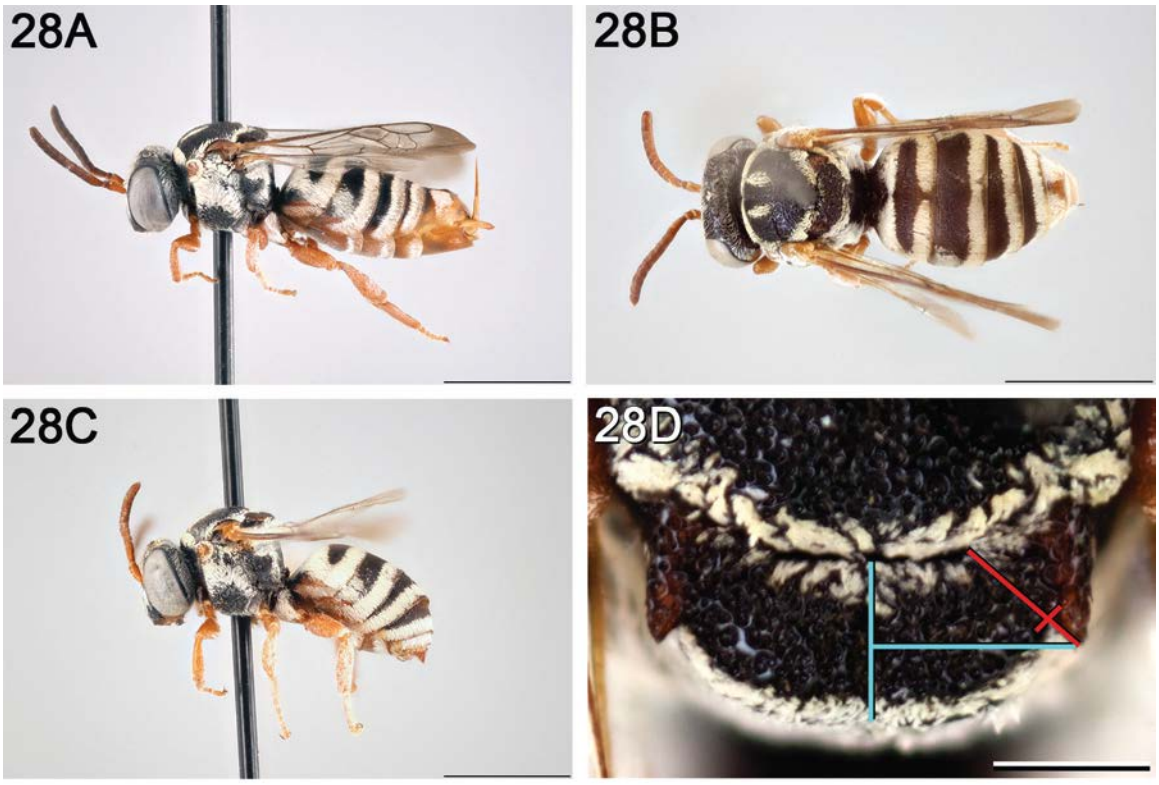


**Figure 28.** *Epeolus brumleyi* **A** female paratype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male paratype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

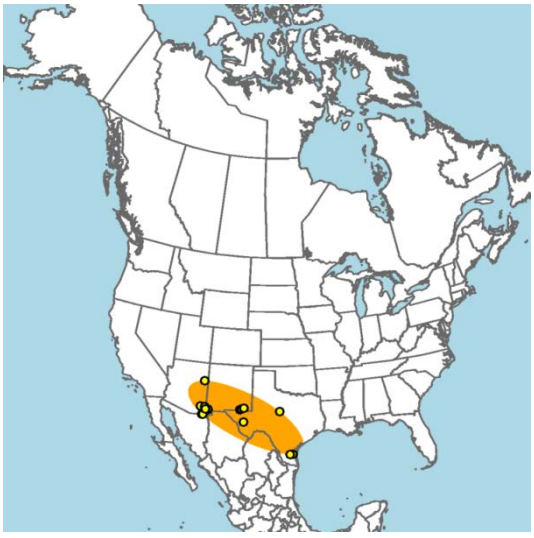

**Figure 29.** Approximate geographic range of *E. brumleyi* (orange) based on occurrence records known to the author (yellow circles).

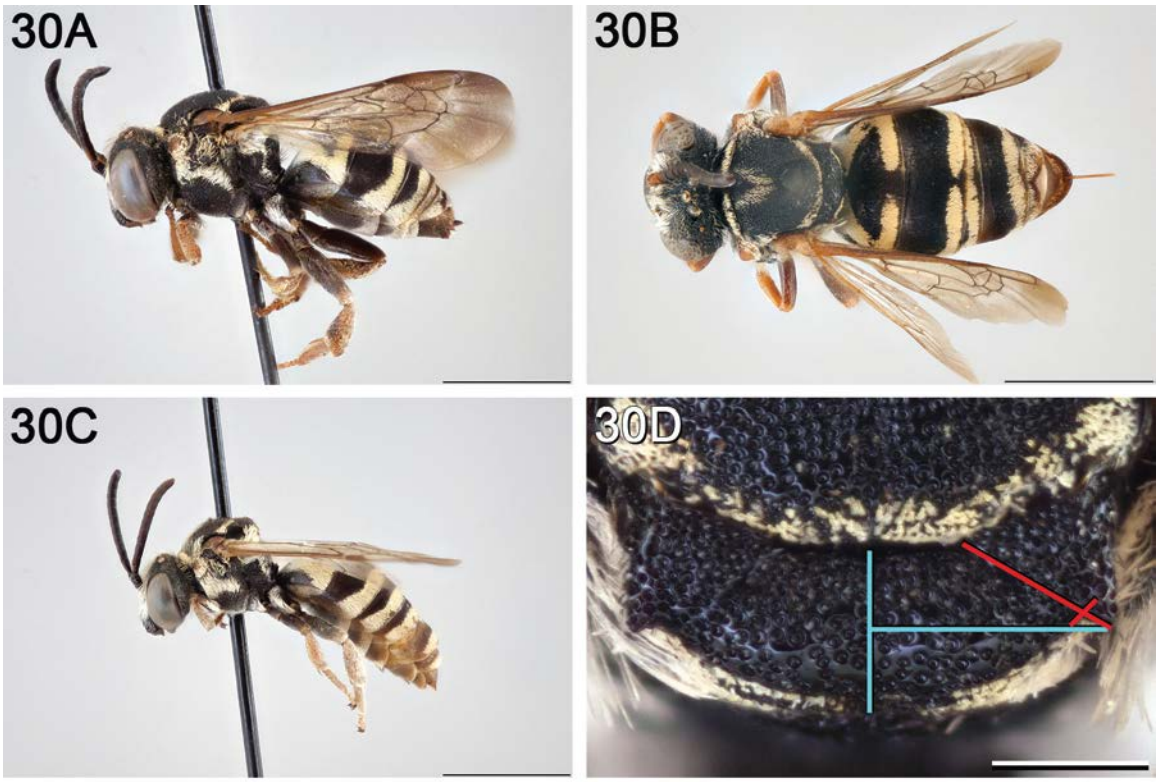


**Figure 30.** *Epeolus canadensis* **A** female, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

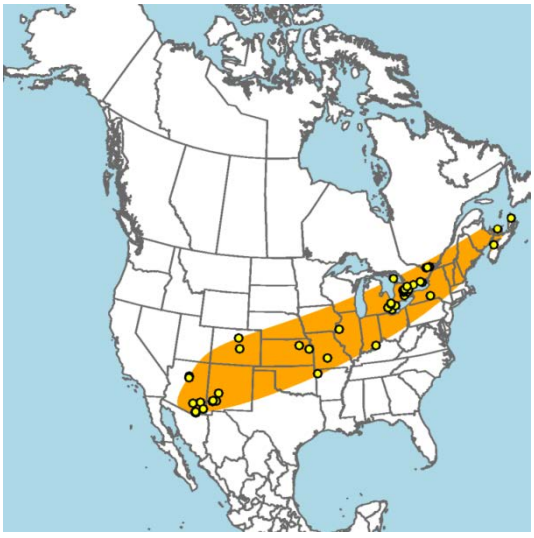

**Figure 31.** Approximate geographic range of *E. canadensis* (orange) based on occurrence records known to the author (yellow circles).

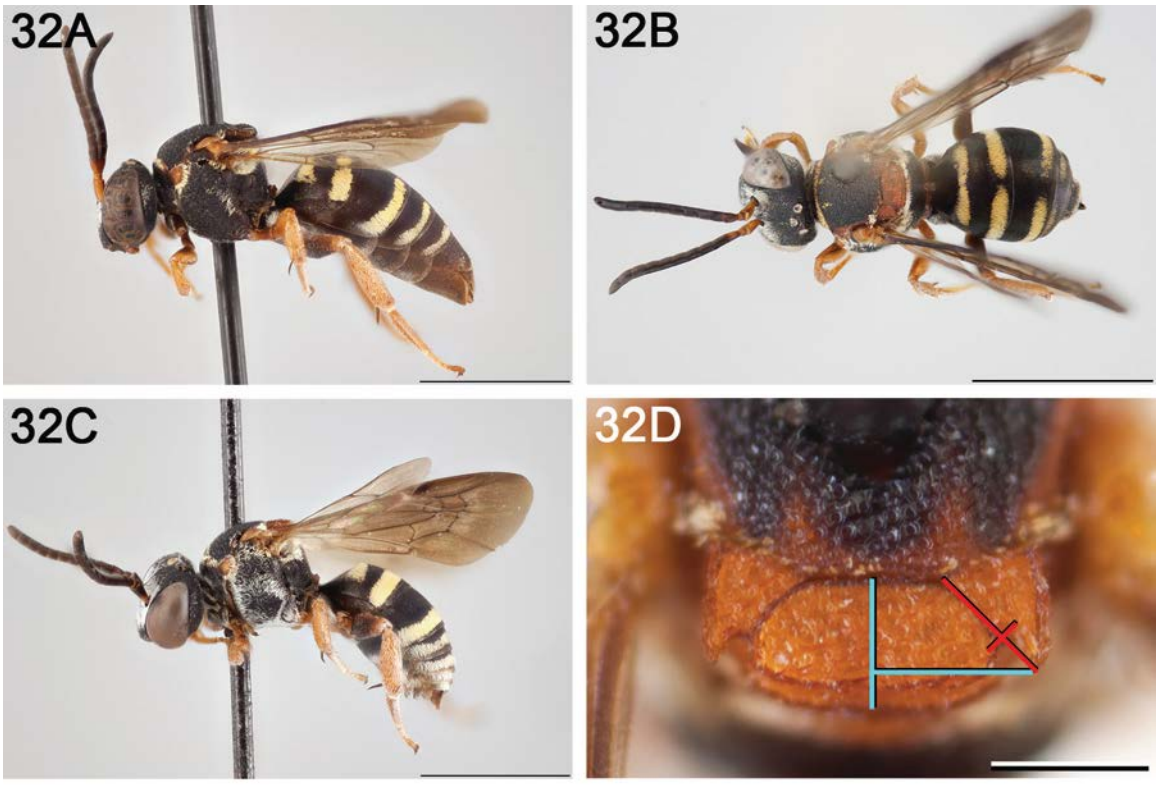


**Figure 32.** *Epeolus carolinus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 33.** Approximate geographic range of *E. carolinus* (orange) based on occurrence records known to the author (yellow circles).

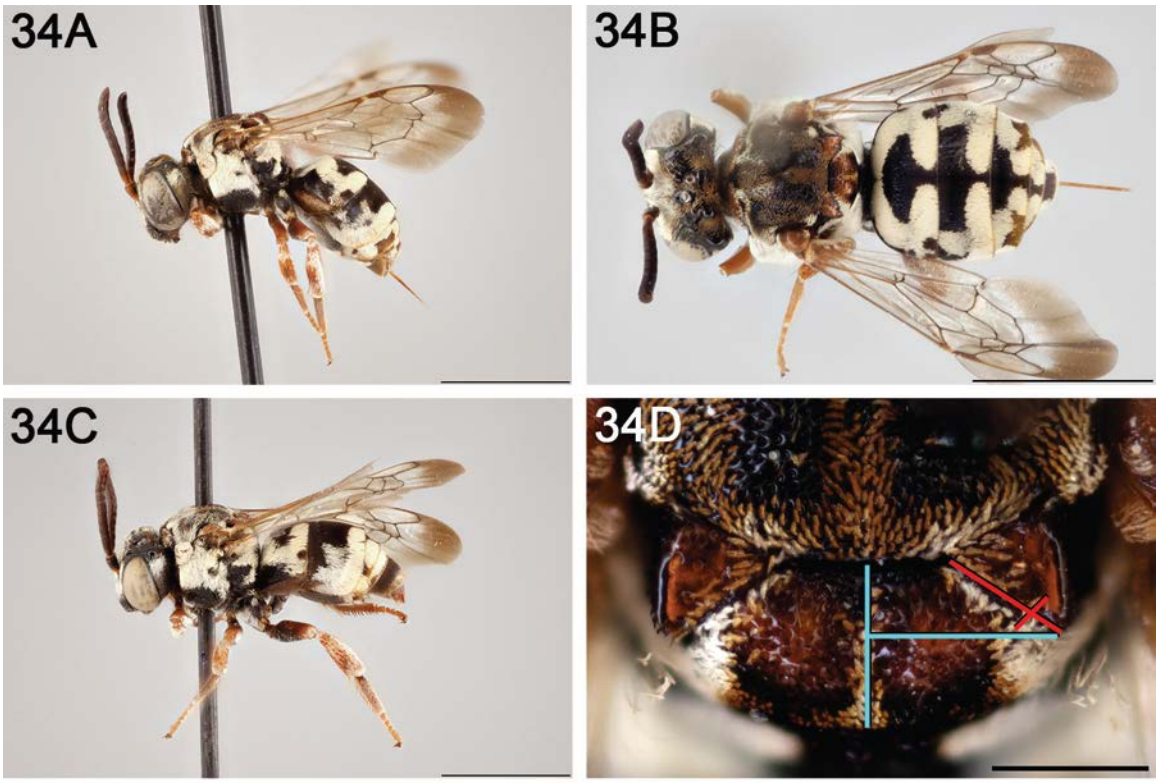


**Figure 34.** *Epeolus chamaesarachae* **A** female paratype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male paratype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

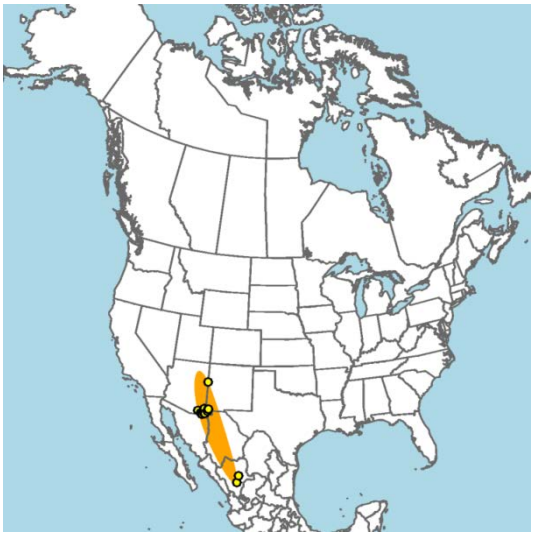

**Figure 35.** Approximate geographic range of *E. chamaesarachae* (orange) based on occurrence records known to the author (yellow circles).


**Figure 36.** *Epeolus compactus* **A** female, lateral habitus (scale bar 3 mm), **B** female lectotype, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

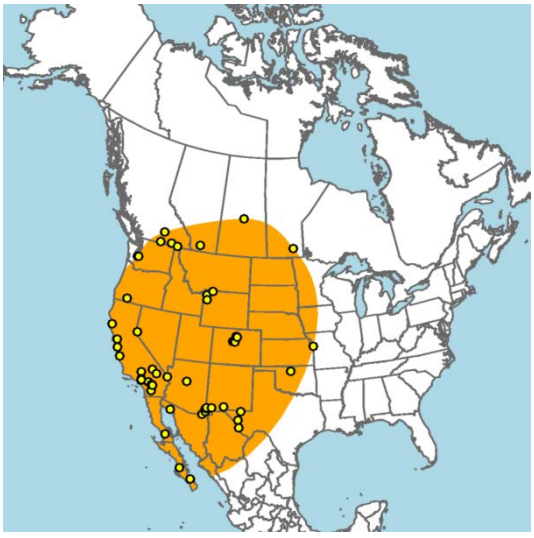

**Figure 37.** Approximate geographic range of *E. compactus* (orange) based on occurrence records known to the author (yellow circles).


**Figure 38. A** *E. crucis* female holotype (herein synonymized under *E. compactus*), dorsal habitus, and **B** *E. compactus* typical female, dorsal habitus, in which the axilla, mesoscutellum, and discs of the metasomal terga (in terms of integument coloration and pubescence) are black or nearly black. Scale bars 3 mm.

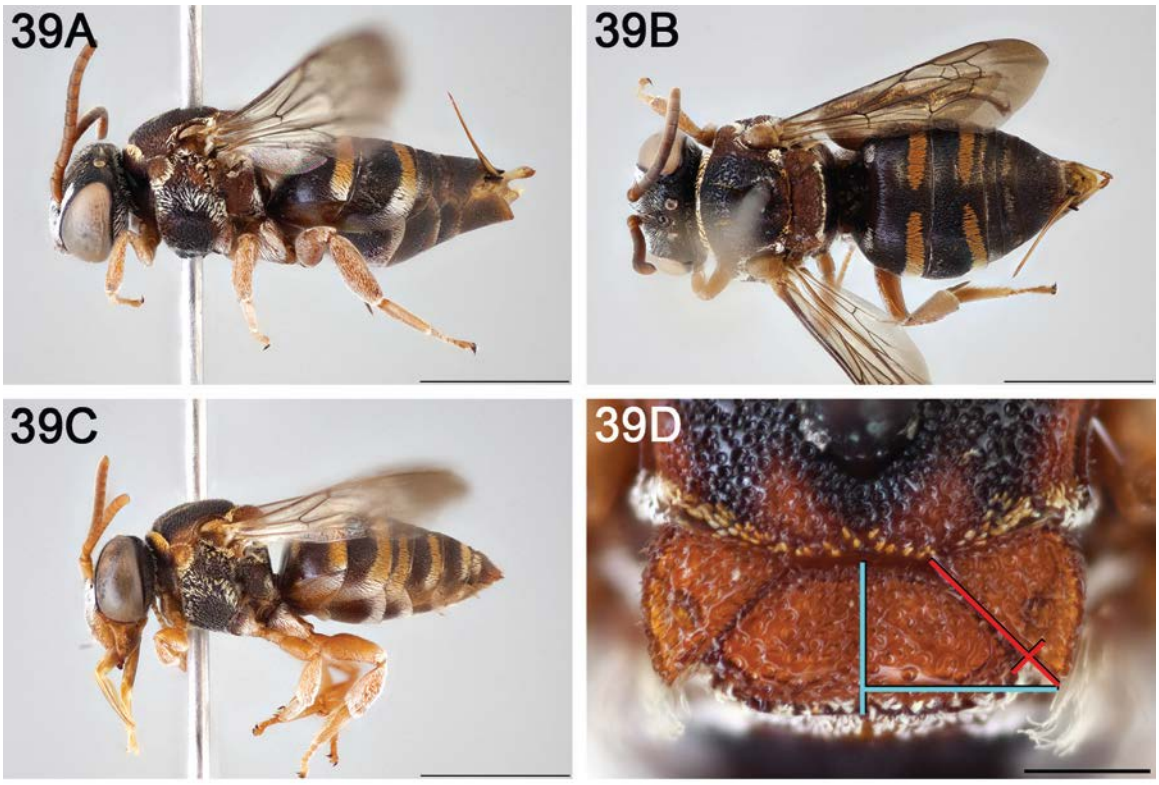


**Figure 39.** *Epeolus deyrupi* **A** female holotype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male allotype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 40.** Occurrence records of *E. deyrupi* known to the author (yellow circles).

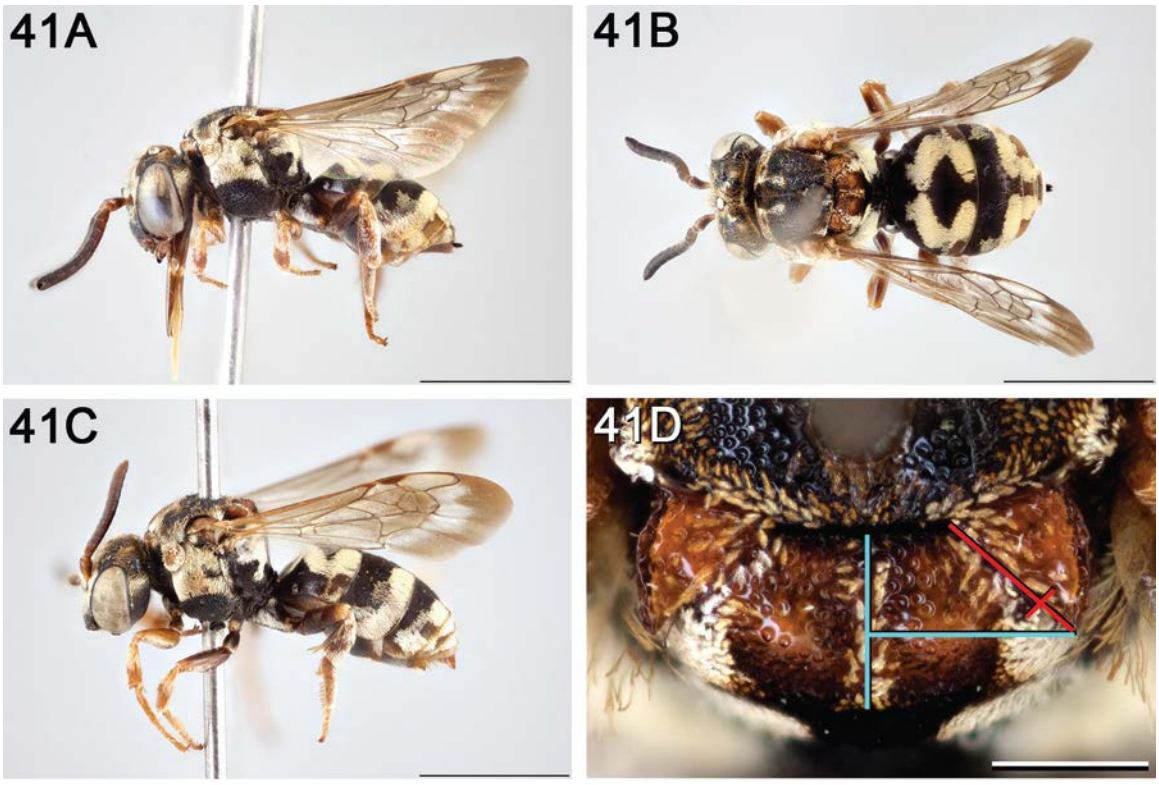


**Figure 41.** *Epeolus diadematus* **A** female holotype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male paratype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 42.** Approximate geographic range of *E. diadematus* (orange) based on occurrence records known to the author (yellow circles).

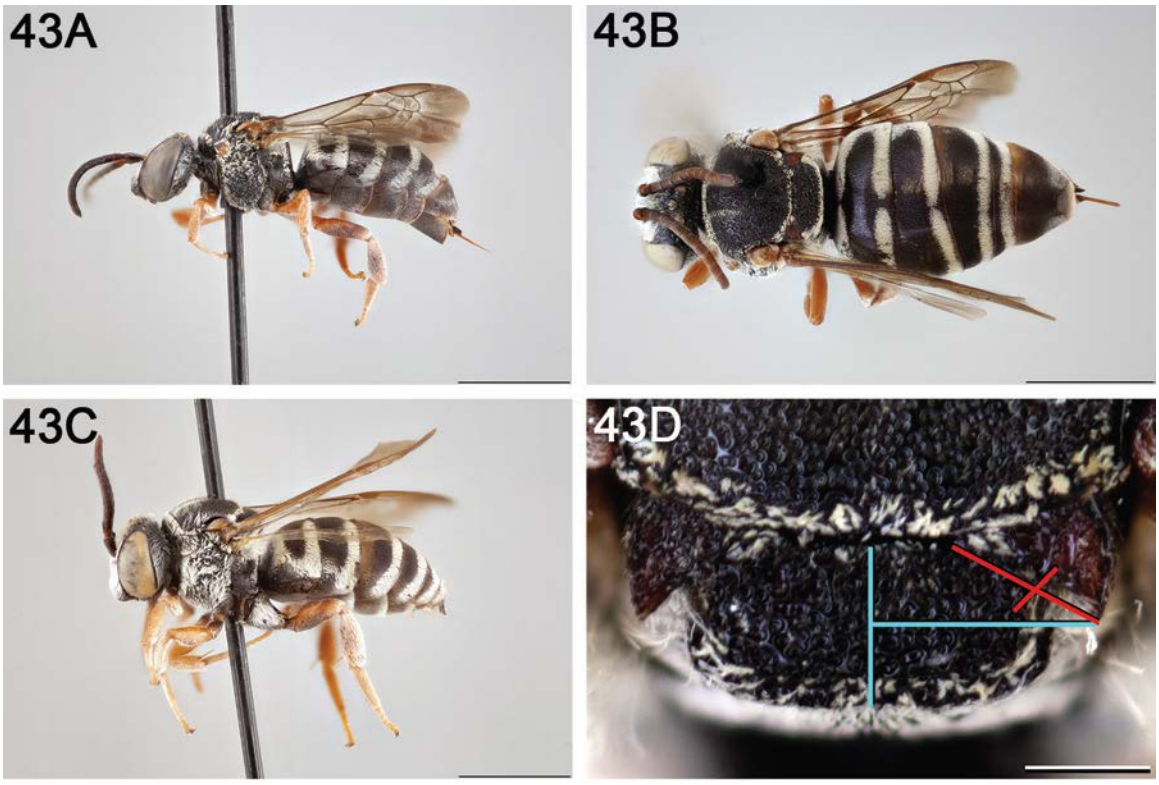


**Figure 43.** *Epeolus erigeronis* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 44.** Approximate geographic range of *E. erigeronis* (orange) based on occurrence records known to the author (yellow circles).

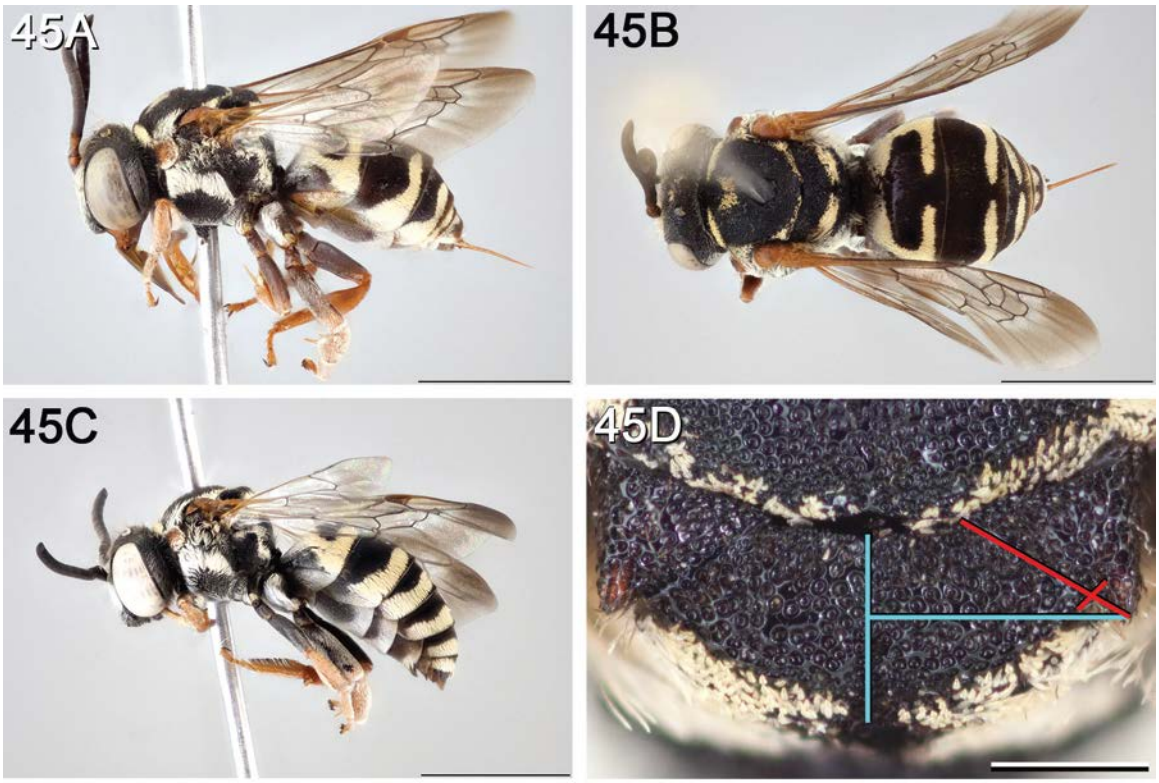


**Figure 45.** *Epeolus ferrarii* **A** female allotype, lateral habitus (scale bar 3 mm), **B** female allotype, dorsal habitus (scale bar 3 mm), **C** male holotype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 46.** Approximate geographic range of *E. ferrarii* (orange) based on occurrence records known to the author (yellow circles).

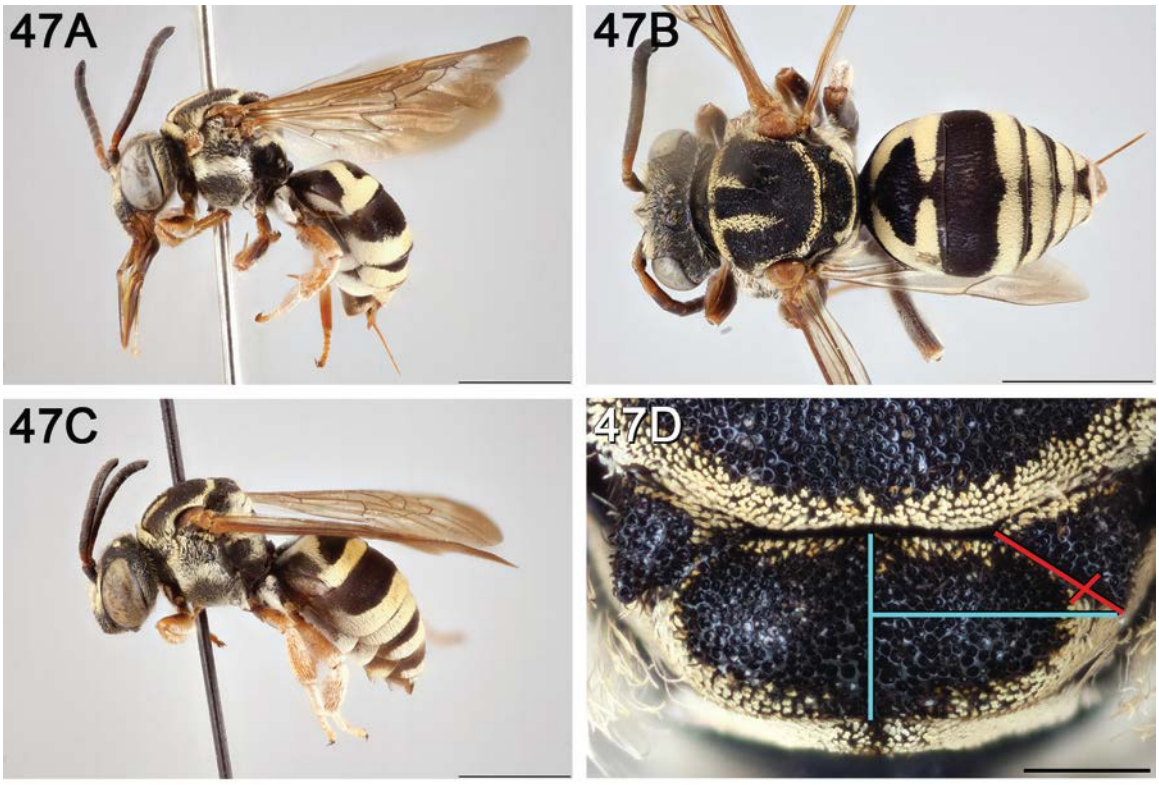


**Figure 47.** *Epeolus flavofasciatus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 48.** Approximate geographic range of *E. flavofasciatus* (orange) based on occurrence records known to the author (yellow circles).

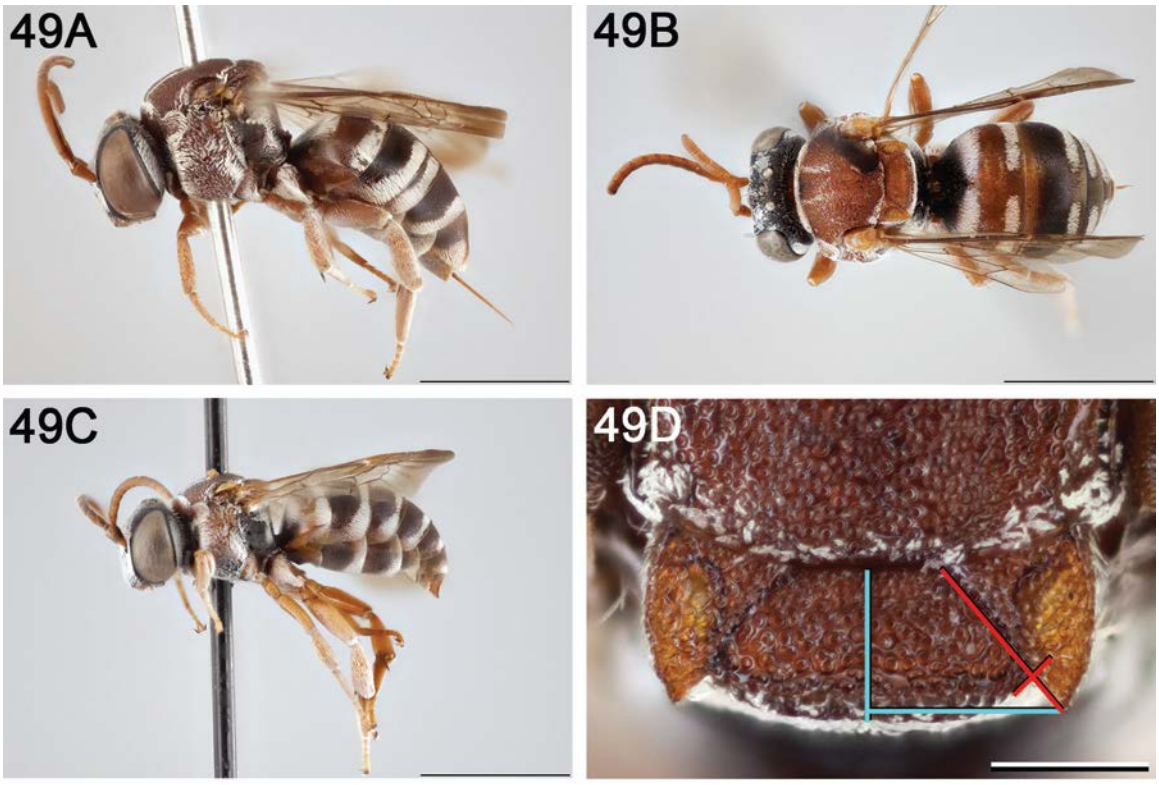


**Figure 49.** *Epeolus floridensis* **A** female, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 50.** Occurrence records of *E. floridensis* known to the author (yellow circles).

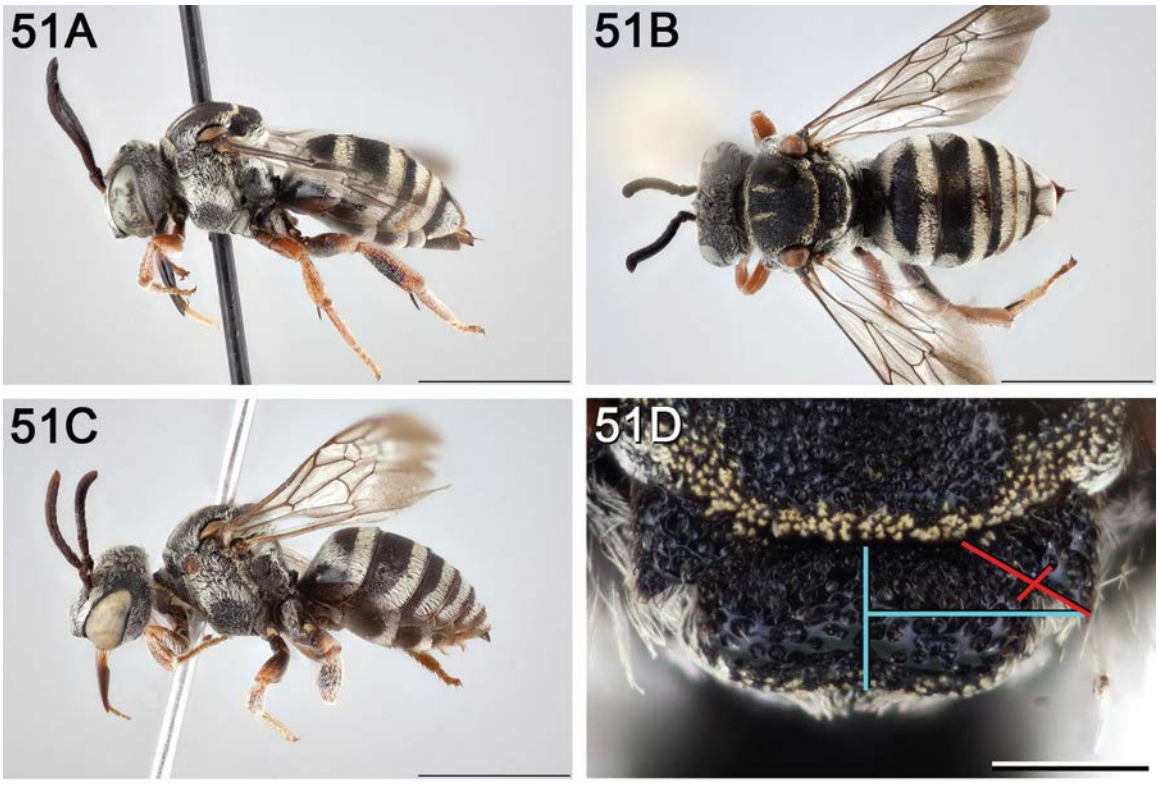


**Figure 51.** *Epeolus gibbsi* **A** female holotype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male allotype, lateral habitus (scale bar 3 mm), and **D** female holotype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 52.** Occurrence records of *E. gibbsi* known to the author (yellow circles).

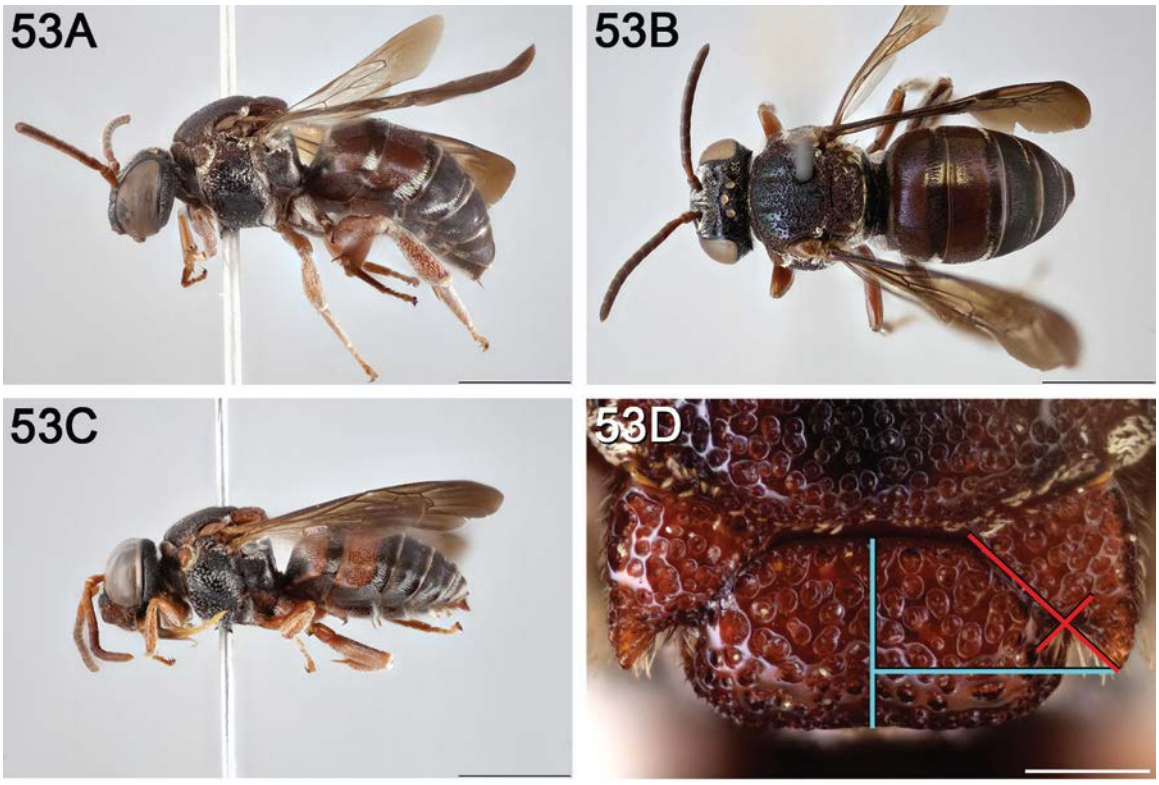


**Figure 53.** *Epeolus glabratus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 54.** Approximate geographic range of *E. glabratus* (orange) based on occurrence records known to the author (yellow circles).

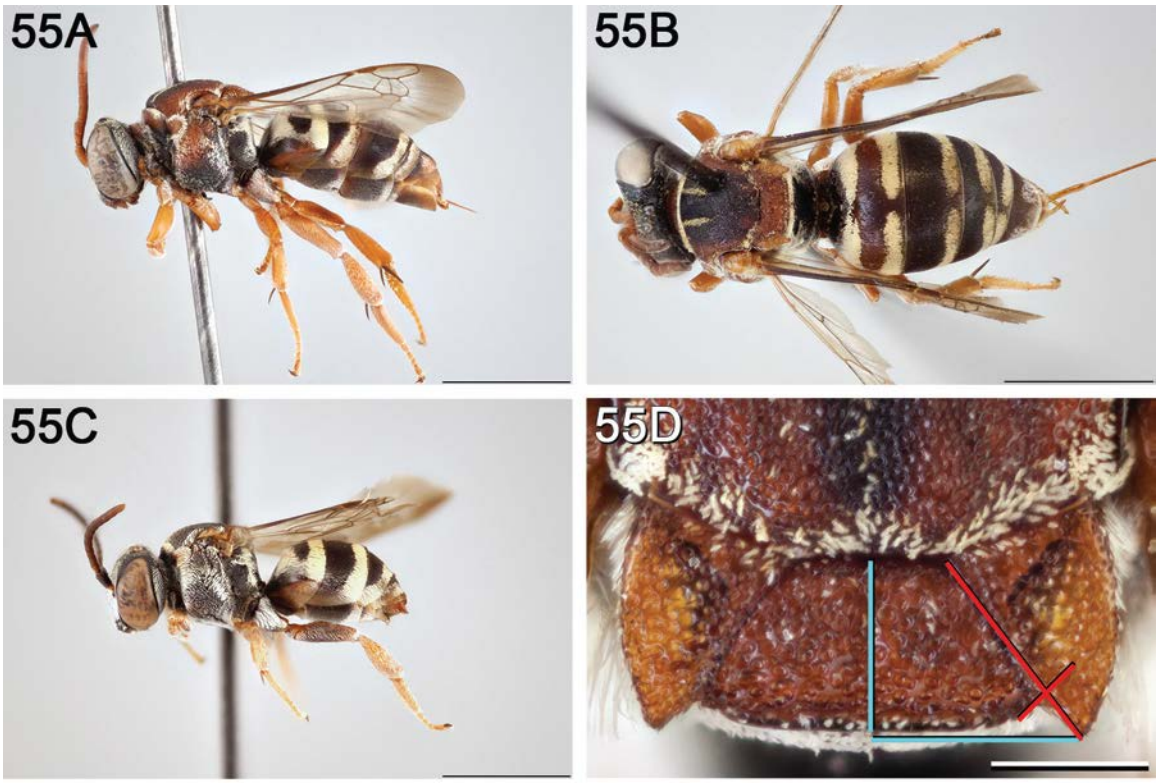


**Figure 55.** *Epeolus howardi* **A** female, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 56.** Approximate geographic range of *E. howardi* (orange) based on occurrence records known to the author (yellow circles).

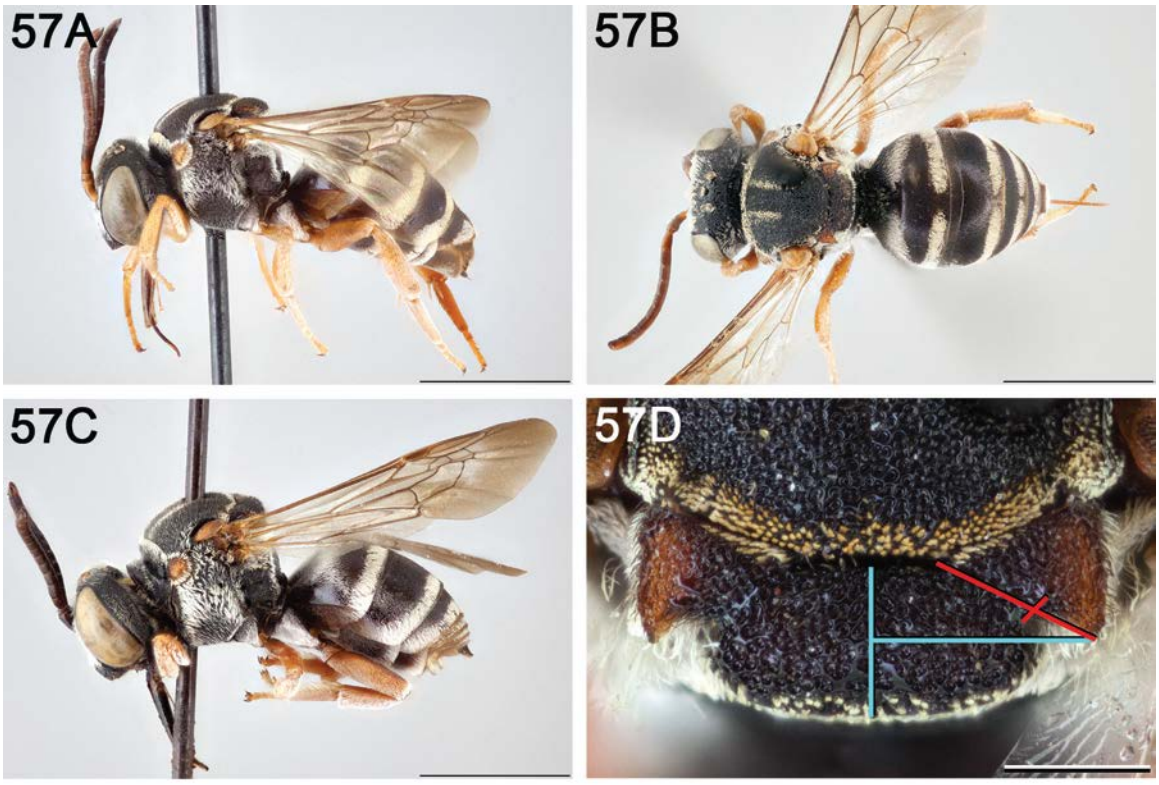


**Figure 57.** *Epeolus ilicis* **A** female, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male paratype, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum (photo of *E. vernalis* holotype), dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 58.** Approximate geographic range of *E. ilicis* (orange) based on occurrence records known to the author (yellow circles).

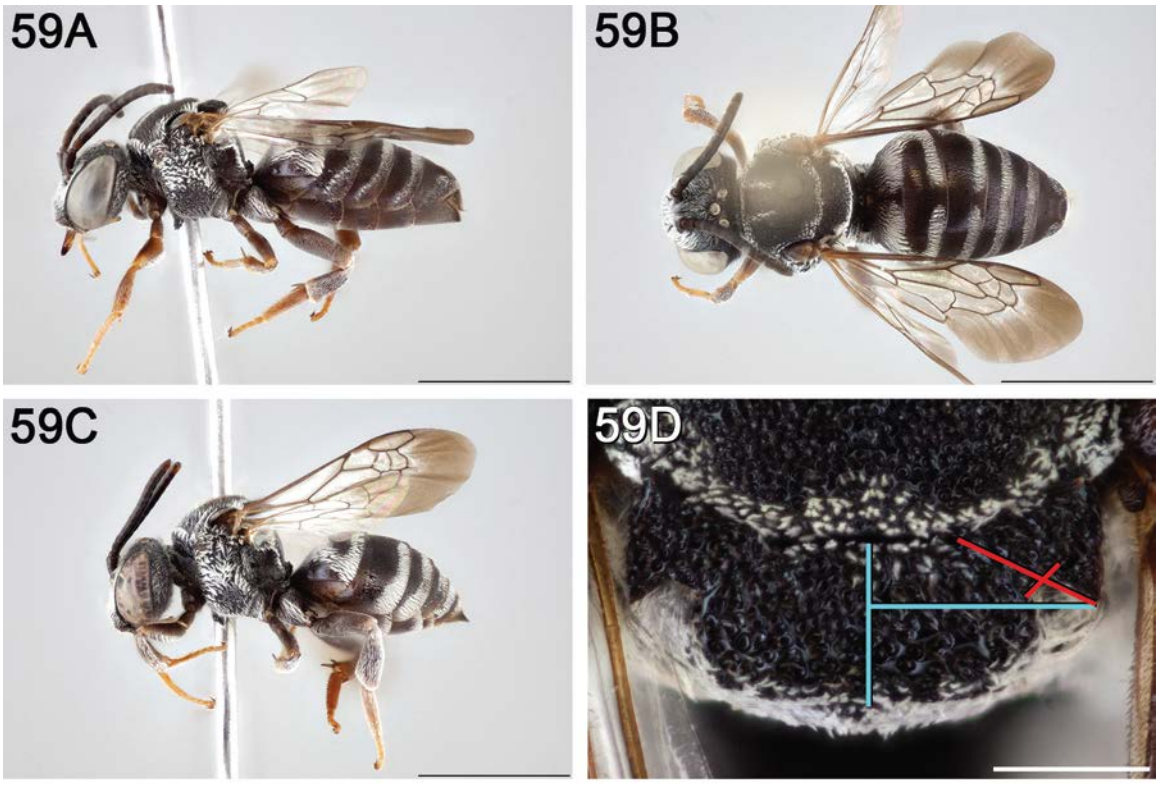


**Figure 59.** *Epeolus inornatus* **A** female holotype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male allotype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 60.** Approximate geographic range of *E. inornatus* (orange) based on occurrence records known to the author (yellow circles).

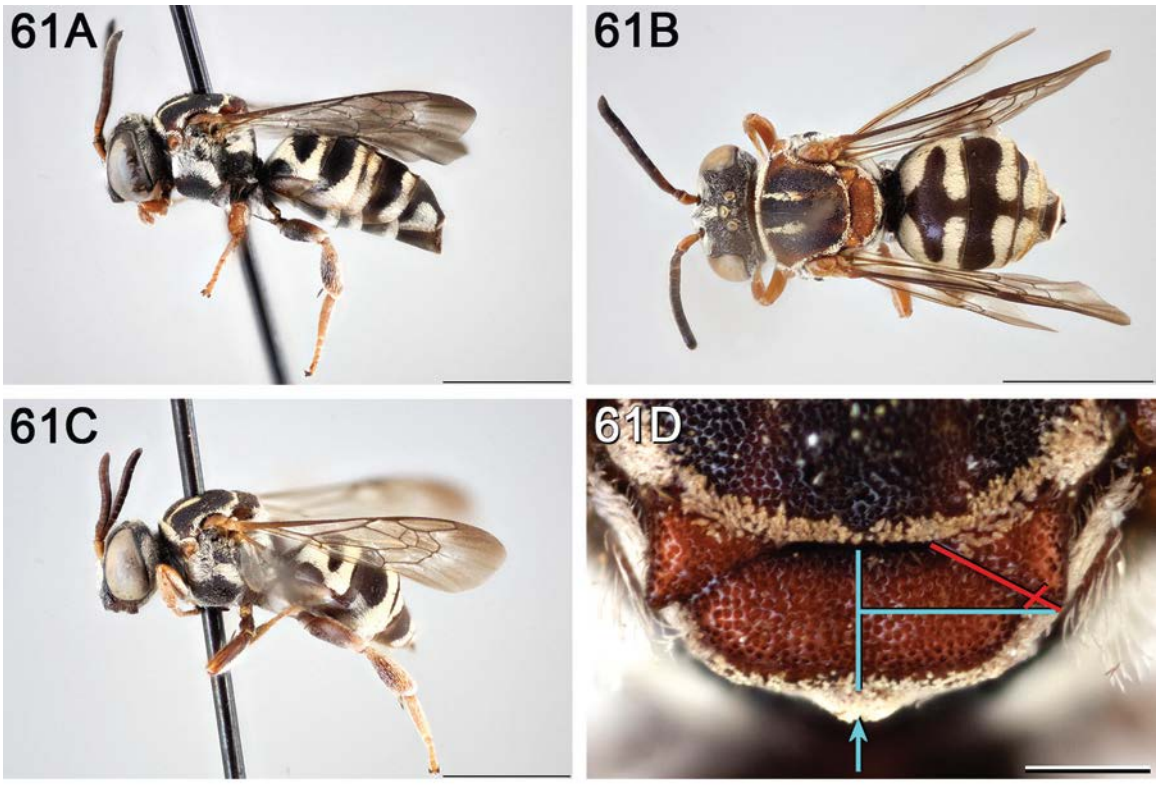


**Figure 61.** *Epeolus interruptus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue arrow indicates process of metanotum; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

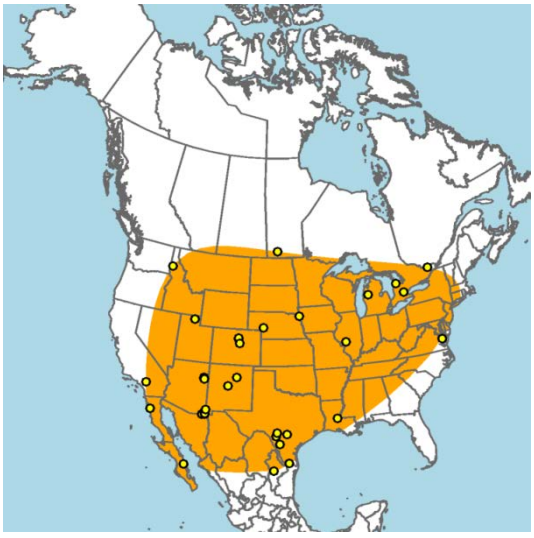

**Figure 62.** Approximate geographic range of *E. interruptus* (orange) based on occurrence records known to the author (yellow circles).

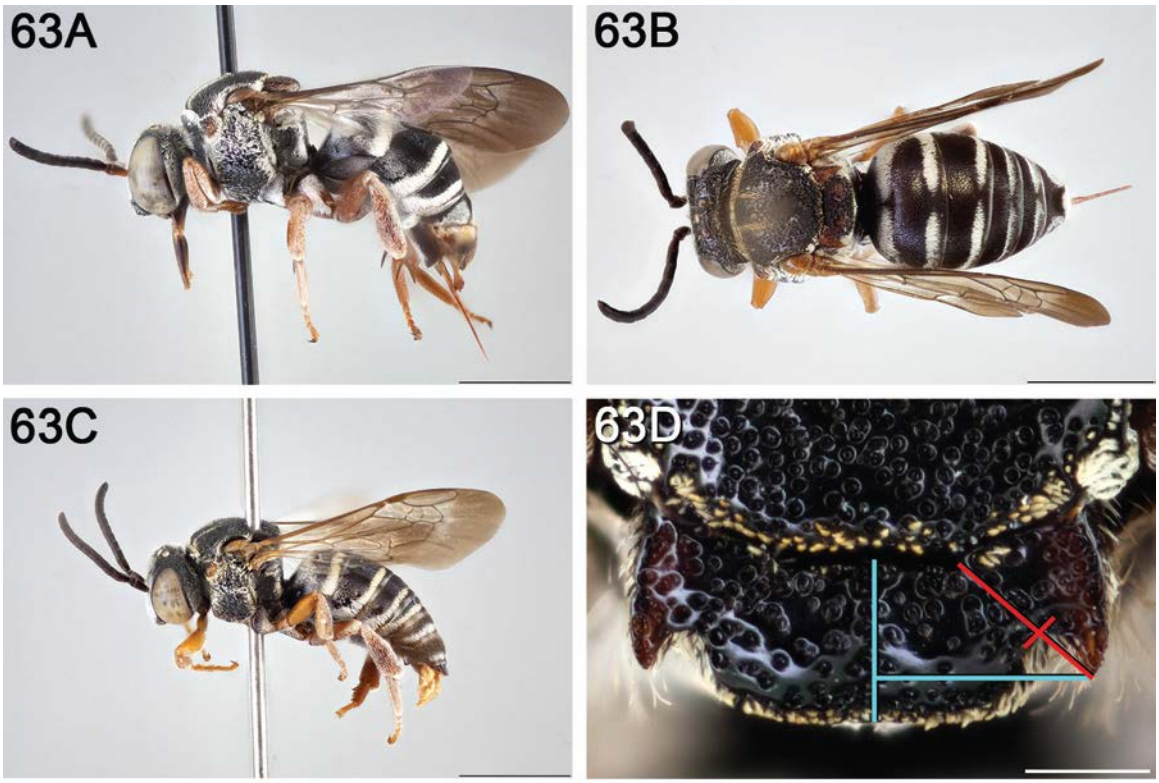


**Figure 63.** *Epeolus lectoides* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 64.** Approximate geographic range of *E. lectoides* (orange) based on occurrence records known to the author (yellow circles).

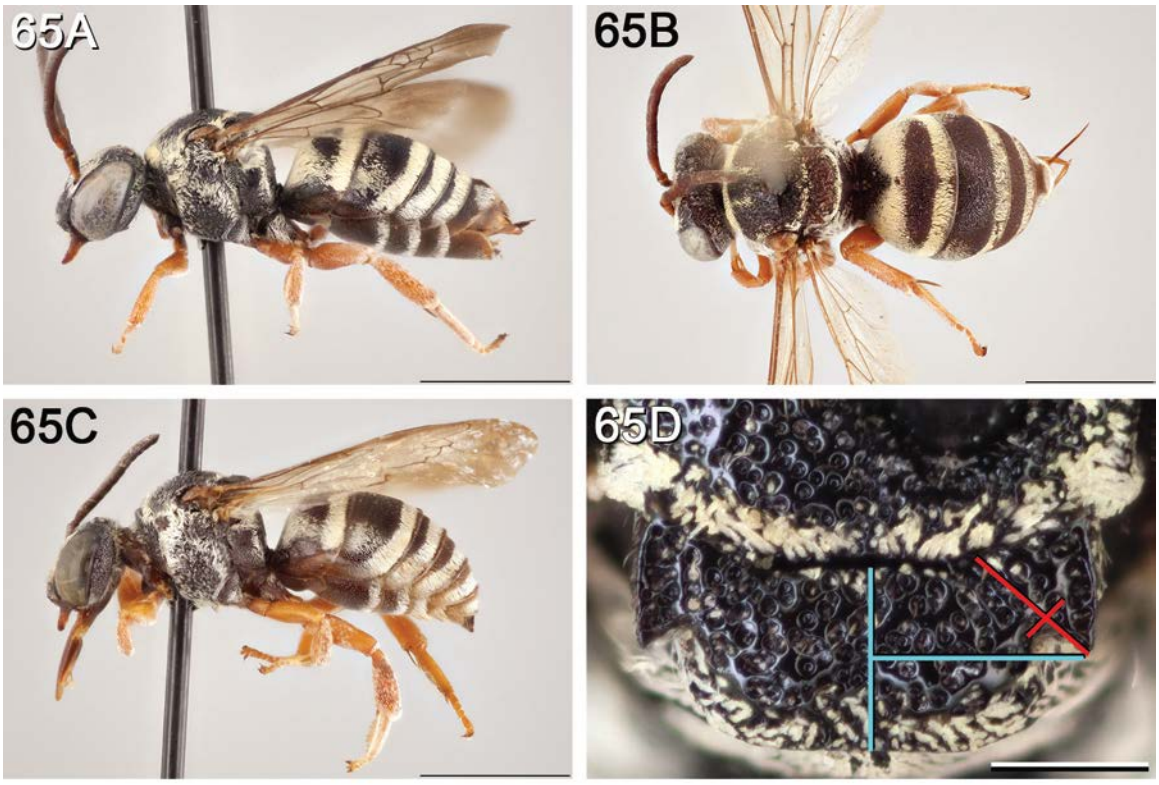


**Figure 65.** *Epeolus lectus* **A** female, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 66.** Approximate geographic range of *E. lectus* (orange) based on occurrence records known to the author (yellow circles).

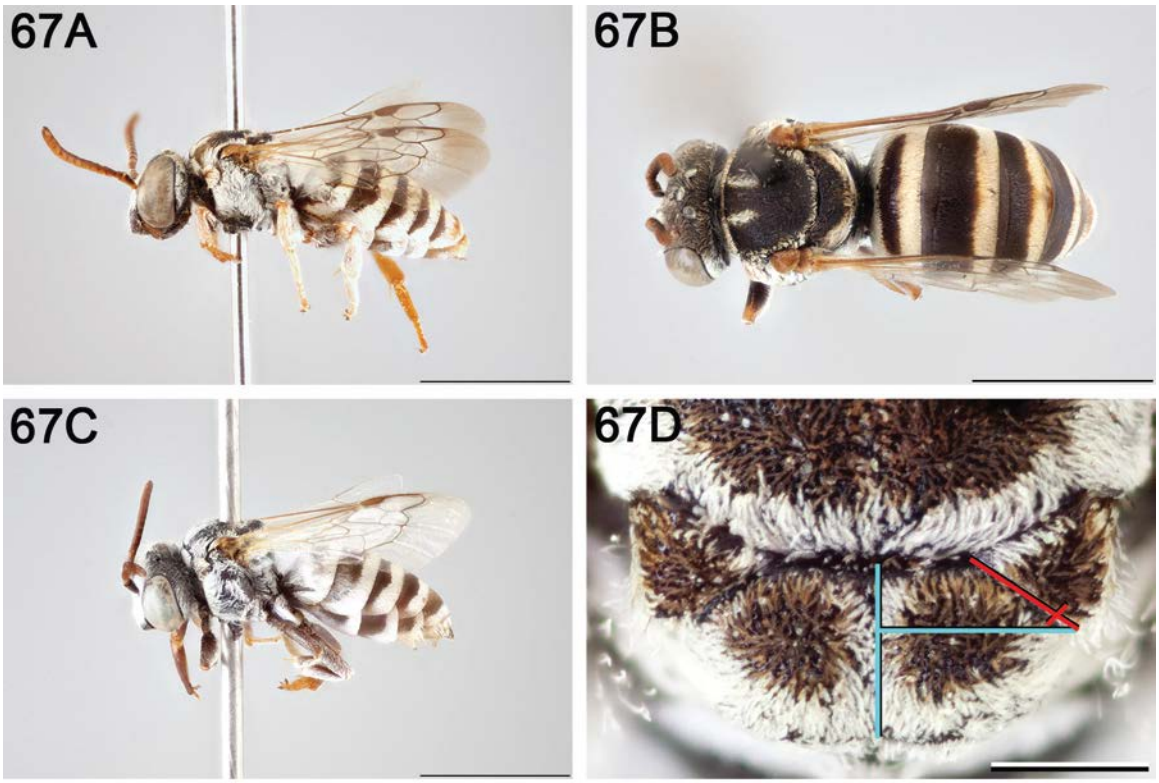


**Figure 67.** *Epeolus mesillae* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male (photo of *P. mesillae* neotype), lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 68.** Approximate geographic range of *E. mesillae* (orange) based on occurrence records known to the author (yellow circles).

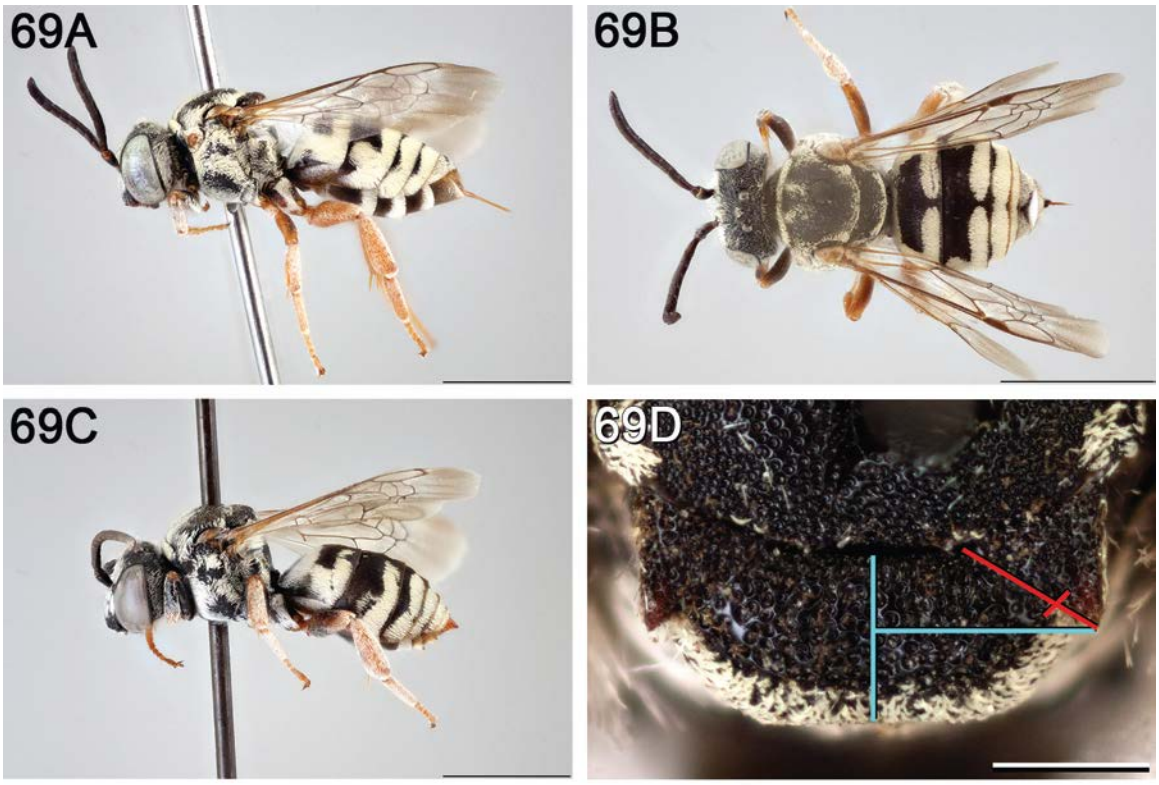


**Figure 69.** *Epeolus minimus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

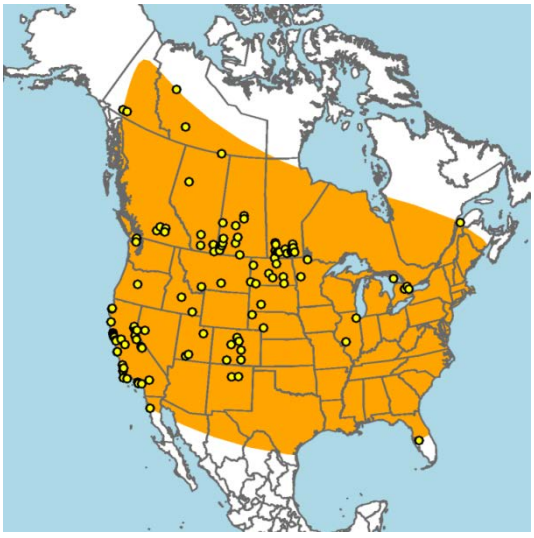

**Figure 70.** Approximate geographic range of *E. minimus* (orange) based on occurrence records known to the author (yellow circles).

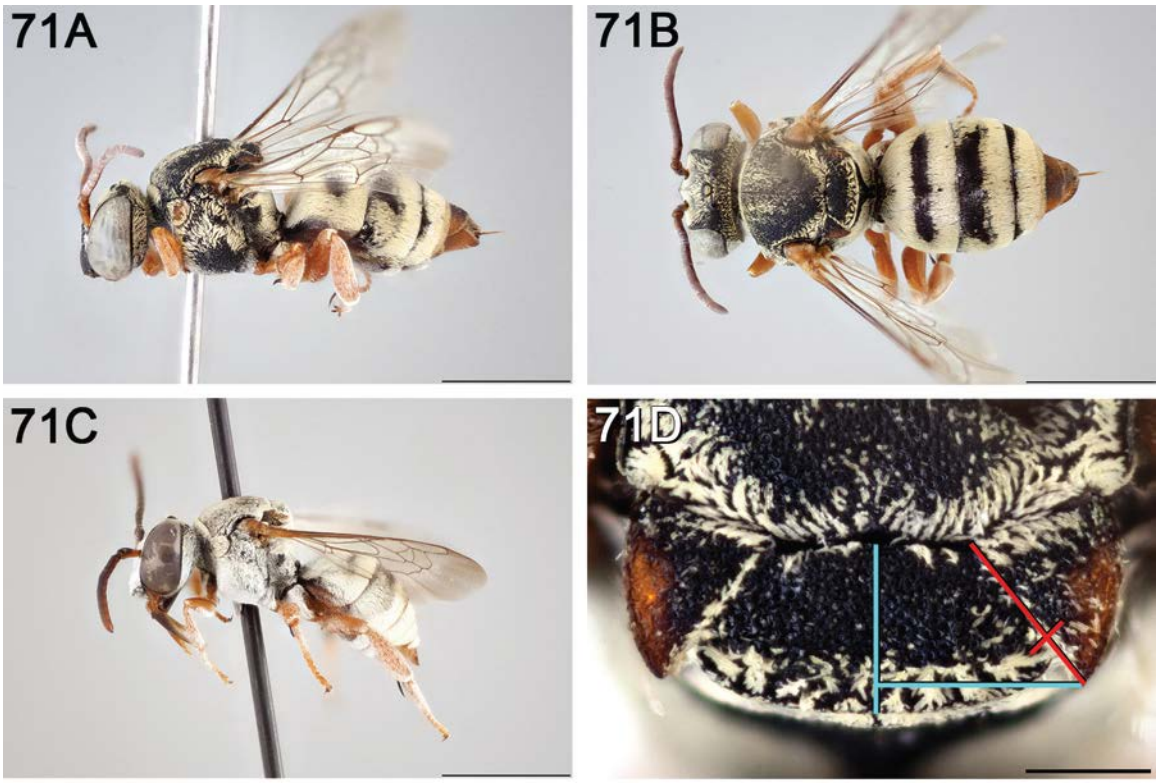


**Figure 71.** *Epeolus nebulosus* **A** female allotype, lateral habitus (scale bar 3 mm), **B** female allotype, dorsal habitus (scale bar 3 mm), **C** male holotype, lateral habitus (scale bar 3 mm), and **D** female allotype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 72.** Occurrence records of *E. nebulosus* known to the author (yellow circles).

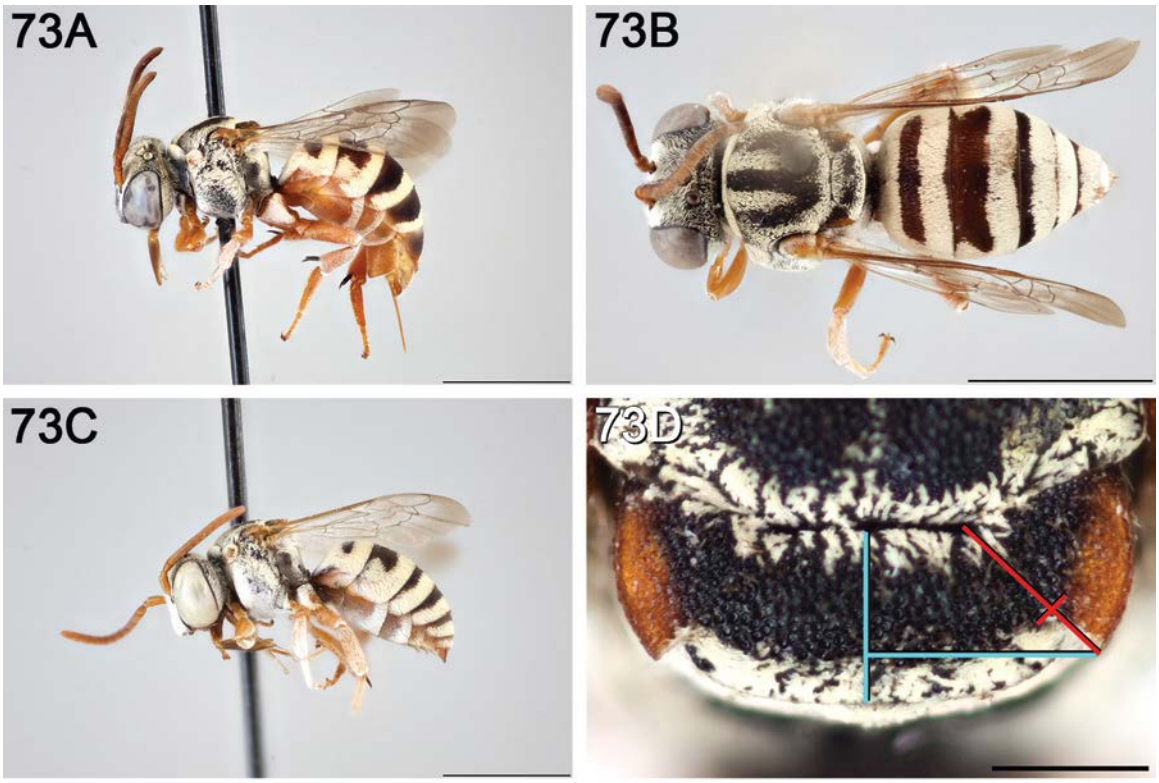


**Figure 73.** *Epeolus novomexicanus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

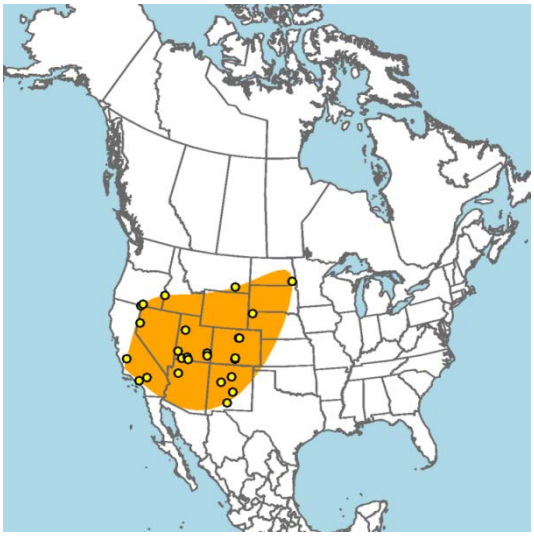

**Figure 74.** Approximate geographic range of *E. novomexicanus* (orange) based on occurrence records known to the author (yellow circles).

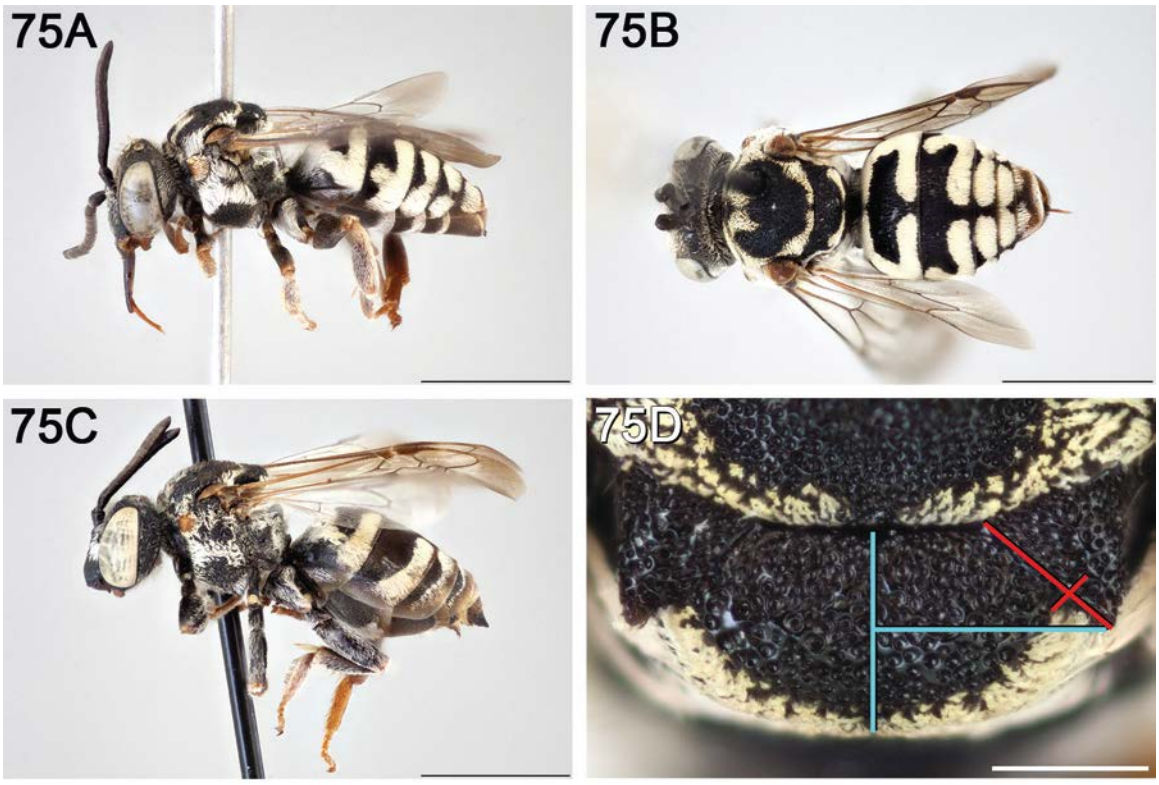


**Figure 75.** *Epeolus olympiellus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 76.** Approximate geographic range of *E. olympiellus* (orange) based on occurrence records known to the author (yellow circles).

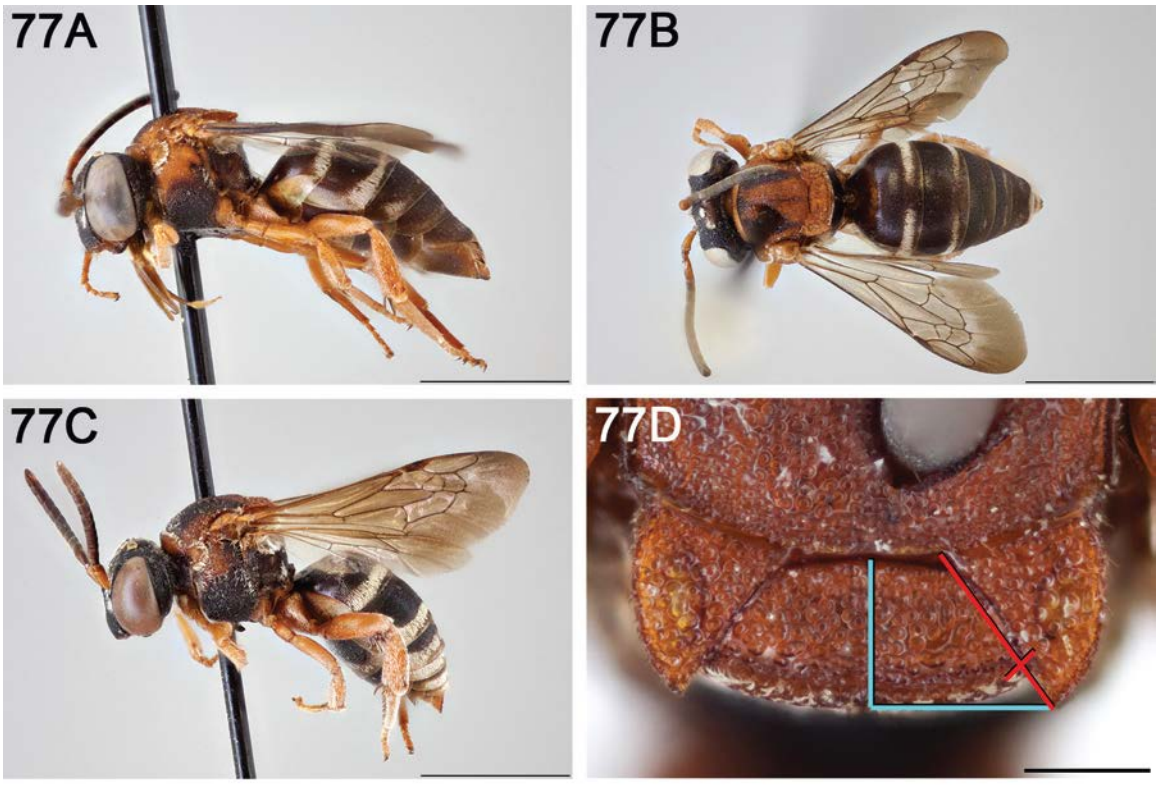


**Figure 77.** *Epeolus packeri* **A** female holotype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male paratype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 78.** Occurrence records of *E. packeri* known to the author (yellow circles).

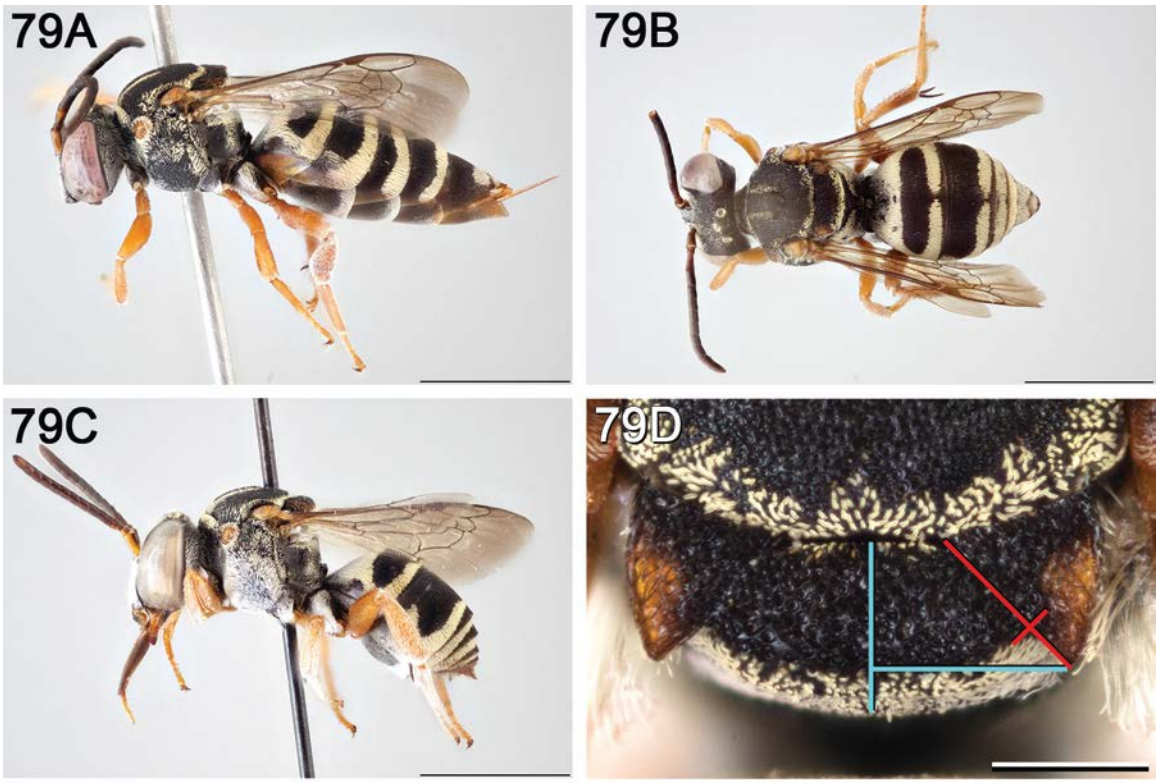


**Figure 79.** *Epeolus pusillus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 80.** Approximate geographic range of *E. pusillus* (orange) based on occurrence records known to the author (yellow circles).

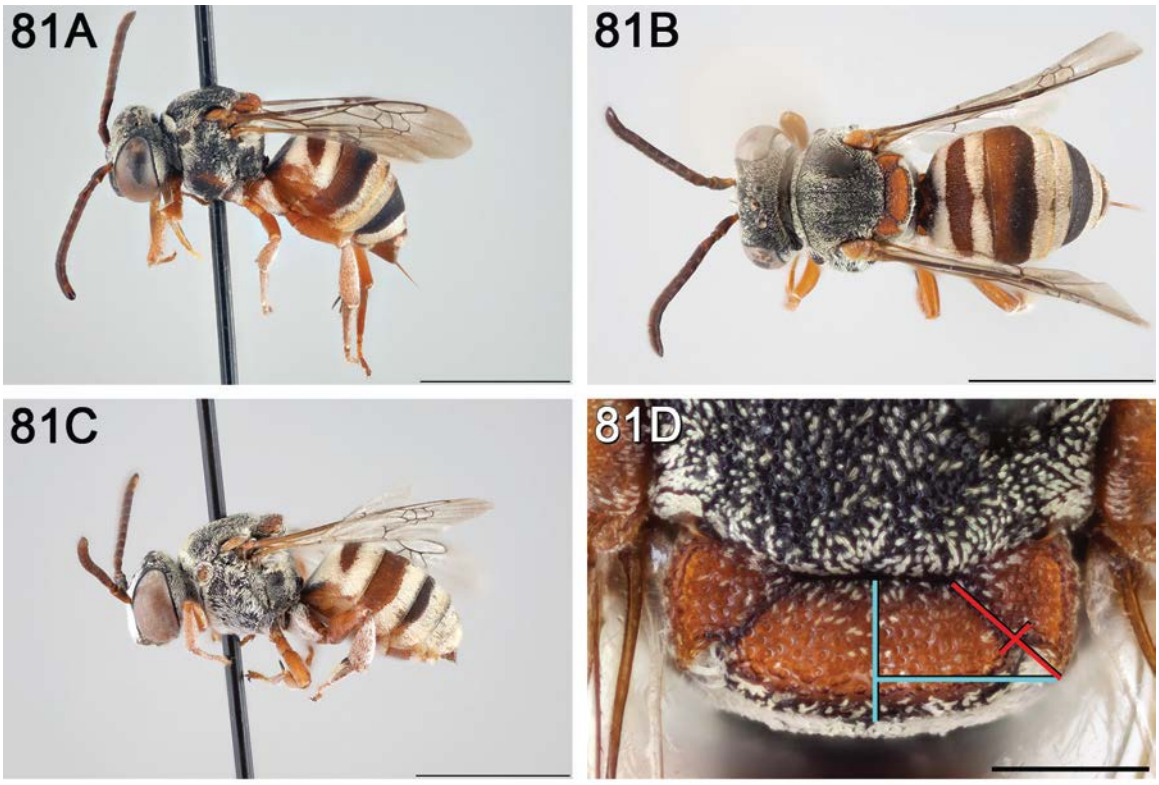


**Figure 81.** *Epeolus rufulus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

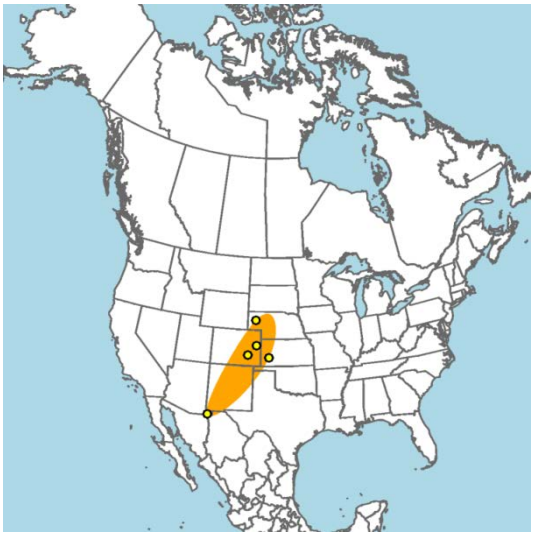

**Figure 82.** Approximate geographic range of *E. rufulus* (orange) based on occurrence records known to the author (yellow circles).

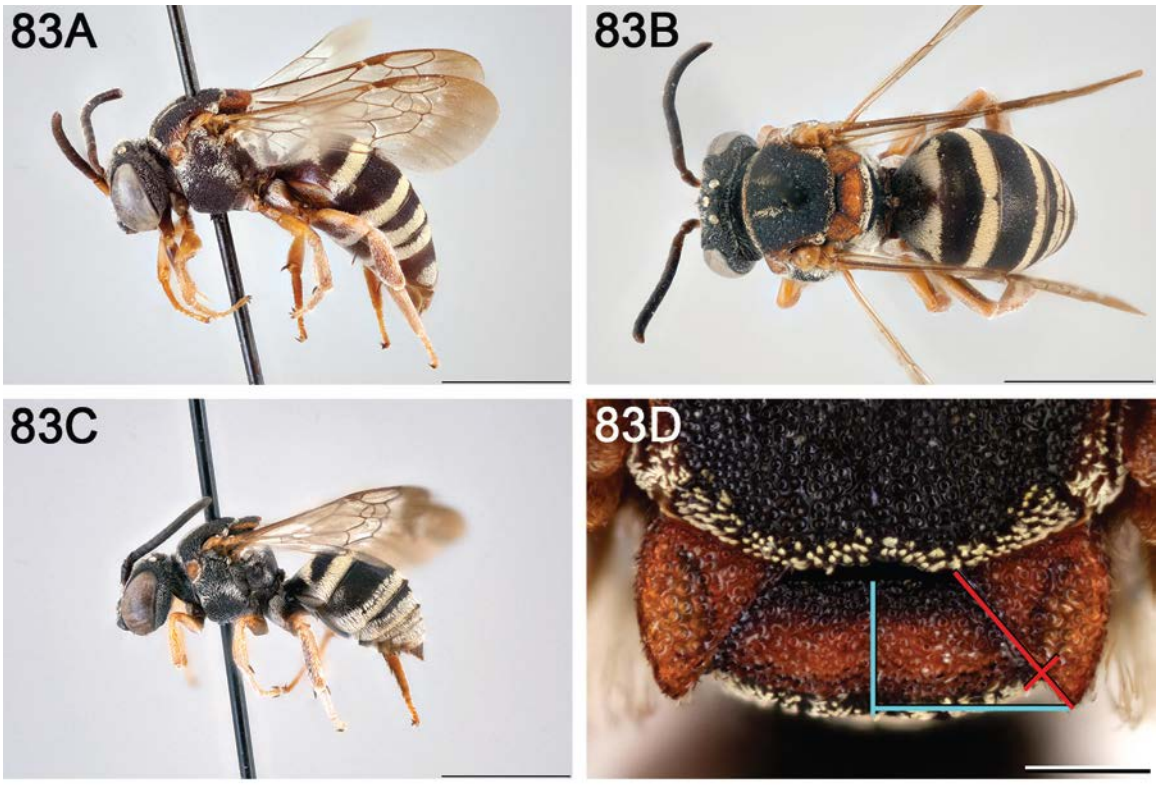


**Figure 83.** *Epeolus scutellaris* **A** female neotype, lateral habitus (scale bar 3 mm), **B** female neotype, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

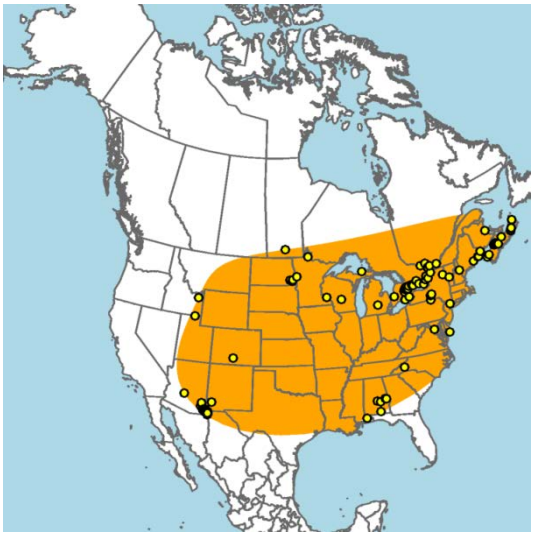

**Figure 84.** Approximate geographic range of *E. scutellaris* (orange) based on occurrence records known to the author (yellow circles).

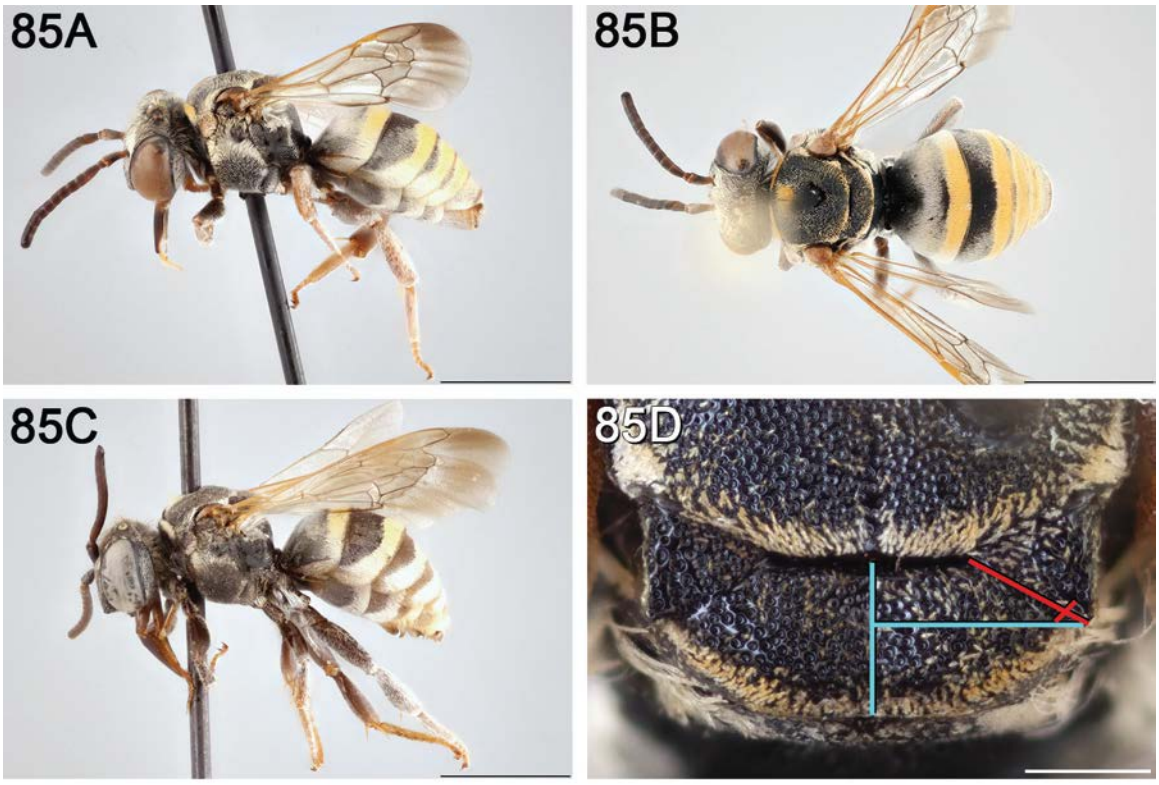


**Figure 85.** *Epeolus splendidus* **A** female holotype, lateral habitus (scale bar 3 mm), **B** female holotype, dorsal habitus (scale bar 3 mm), **C** male paratype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 86.** Approximate geographic range of *E. splendidus* (orange) based on occurrence records known to the author (yellow circles).


**Figure 87.** *Epeolus tessieris* **A** female holotype, lateral habitus (scale bar 3 mm), **B** female paratype, dorsal habitus (scale bar 3 mm), **C** male paratype, lateral habitus (scale bar 3 mm), and **D** female paratype axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 88.** Approximate geographic range of *E. tessieris* (orange) based on occurrence records known to the author (yellow circles).

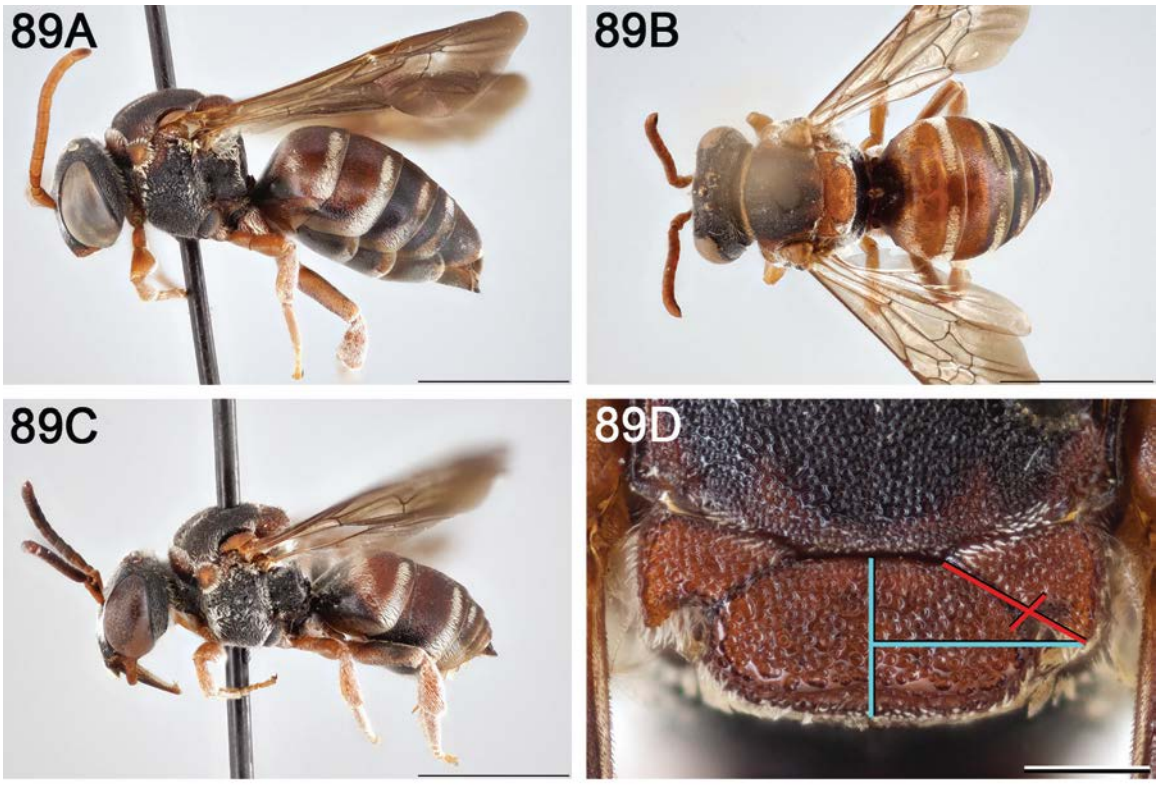


**Figure 89.** *Epeolus zonatus* **A** female, lateral habitus (scale bar 3 mm), **B** female, dorsal habitus (scale bar 3 mm), **C** male, lateral habitus (scale bar 3 mm), and **D** female axillae and mesoscutellum, dorsal view (scale bar 0.5 mm; blue lines indicate the posterior extent of the axilla relative to the length of the mesoscutellum; red lines indicate the extent of the free portion of the axilla relative to its entire medial length).

**Figure 90.** Approximate geographic range of *E. zonatus* (orange) based on occurrence records known to the author (yellow circles).

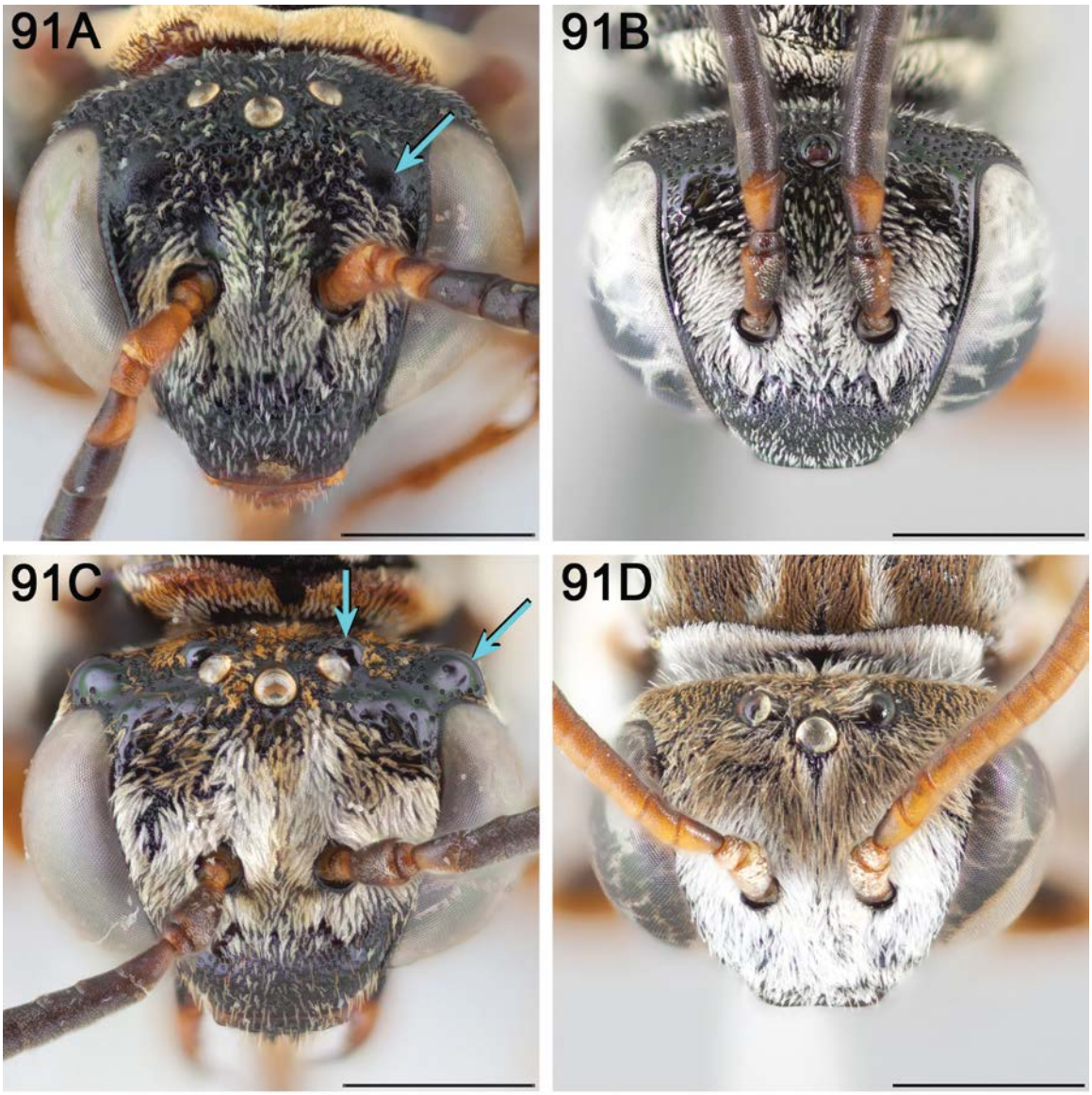


**Figure 91.** Head of female **A** *E. bifasciatus* showing frontal area with pair of granulose protrusions, **B** *E. lectus* showing frontal area without protrusions, **C** *E. chamaesarachae* paratype showing vertexal area with four shiny, impunctate protrusions, and **D** *E. mesillae* showing vertexal area without protrusions. Scale bars 1 mm.

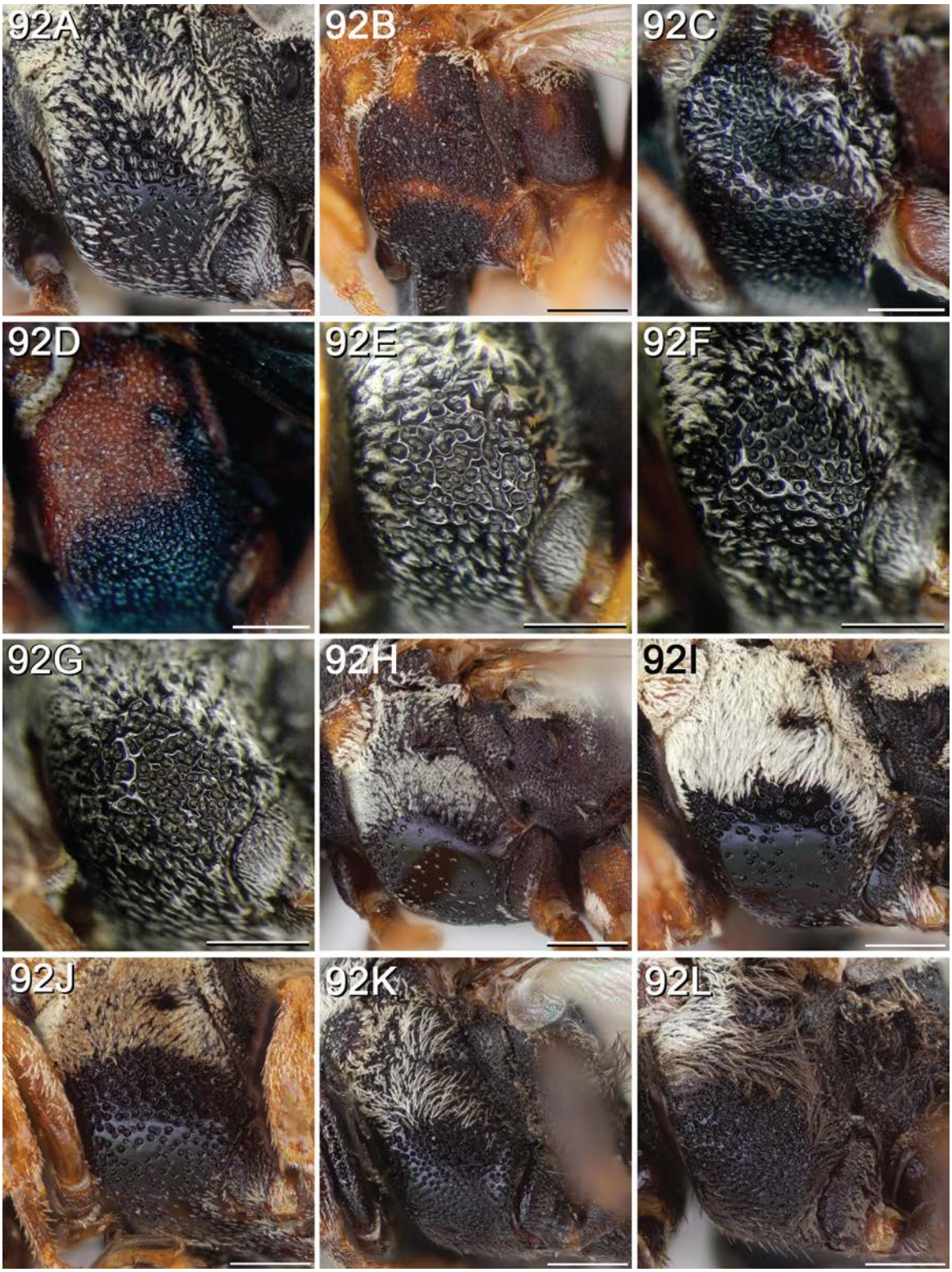


**Figure 92.** Mesopleuron (lateral view) of female **A** *E. lectus* showing sparse punctation (most i>1d); **B** *E. carolinus* showing dense punctation (most i≤1d); **C** *E. deyrupi* paratype showing moderately sparse punctation (i≤2d); **D** *E. packeri* paratype showing moderately dense

punctation (most i<1d); **E** *E. erigeronis* showing very dense punctation (few if any interspaces as large as puncture diameters); **F** *E. ilicis* showing moderately dense punctation (i≤1d); **G** *E. inornatus* paratype showing moderately dense punctation (i≤1d); **H** *E. tessieris* paratype showing very sparse punctation (most i>1d); **I** *E. chamaesarachae* paratype showing very sparse punctation (most i>1d); **J** *E. diadematus* paratype showing sparse punctation, but punctures denser (many i≤1d) relative to *E. chamaesarachae*; **K** *E. americanus* showing moderately dense punctation, with most punctures clearly separated (i=1d) and the interspaces shining; and **L** *E. asperatus* showing very dense punctation (most i<1d). Scale bars 0.5 mm.


**Figure 93.** T2 (medial portion in dorsal view) of female **A** *E. lectus* with punctures coarse and deep, **B** *E. glabratus* with punctures minutes and shallow, and **C** *E. inornatus* paratype with punctures minute and shallow. Scale bars 0.5 mm.

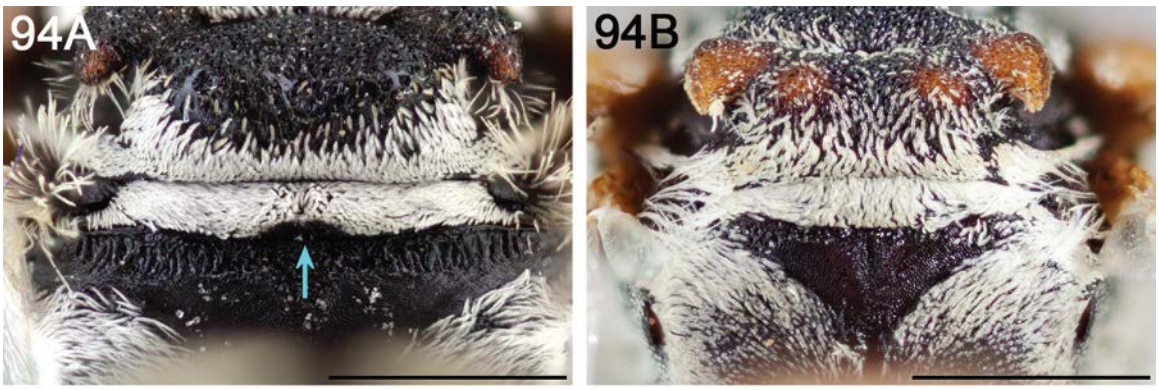


**Figure 94.** Metanotum (in posterior view) of female **A** *E. axillaris* holotype, which has a distinct posteromedial depression, and **B** *E. attenboroughi* paratype, which does not have a depression and is flat. Scale bars 1 mm.

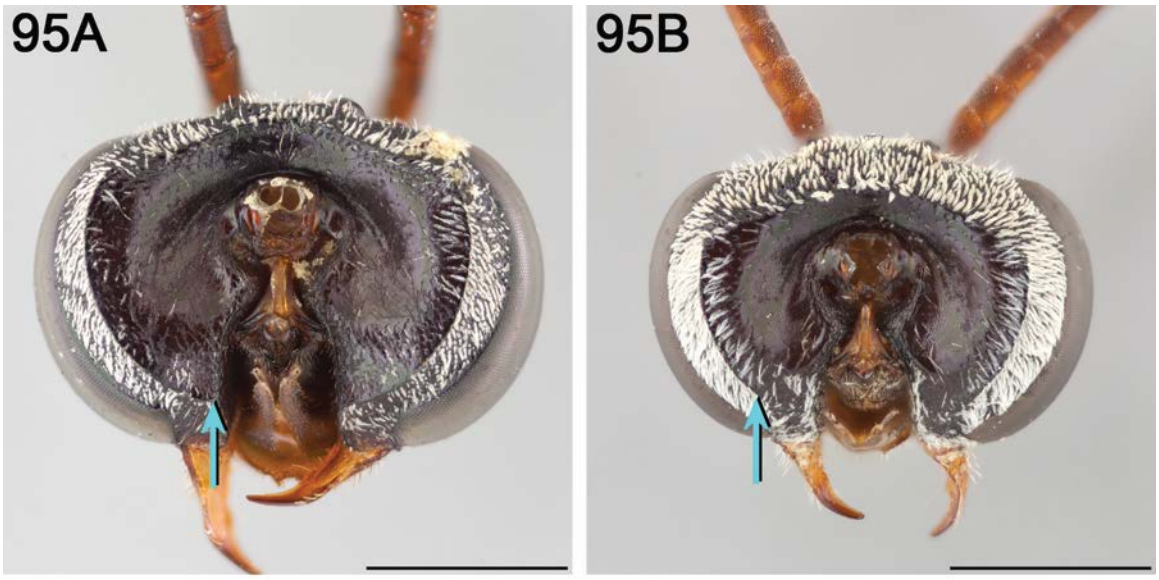


**Figure 95.** Head (in posterior view) removed from female **A** *E. ainsliei*, in which the preoccipital ridge joins the hypostomal carina, and **B** *E. attenboroughi* holotype, in which the preoccipital ridge does not join the hypostomal carina. Scale bars 1 mm. Note that these features can be seen without having to detach the head.

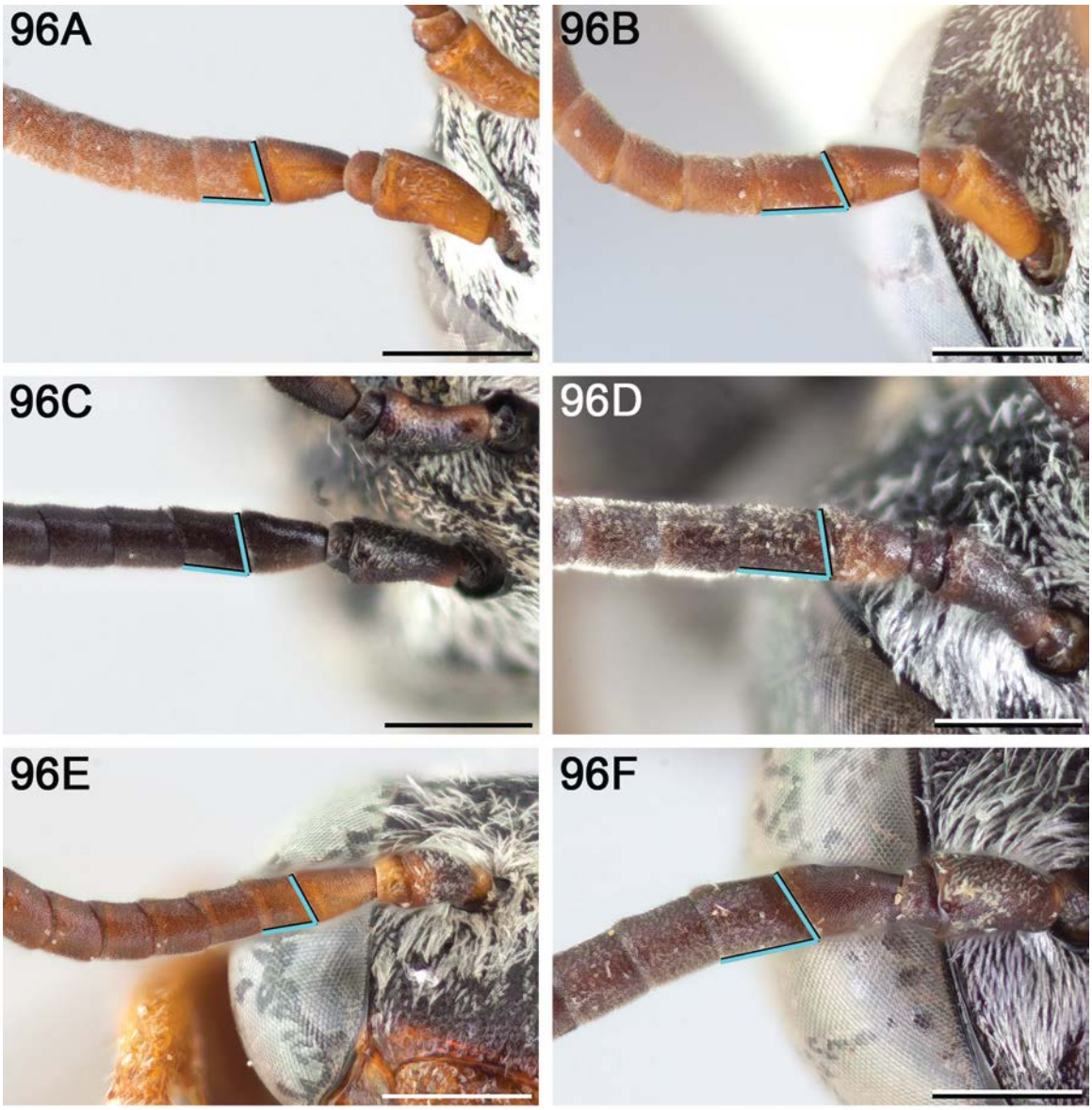


**Figure 96.** Antennae (basal portion) of female *Epeolus* spp. illustrating relative length to width of F2: **A** *E. attenboroughi* paratype, with F2 not noticeably longer than wide, **B** *E. rufulus* holotype, with F2 noticeably longer than wide, **C** *E. gibbsi* holotype, with F2 not noticeably longer than wide, **D** *E. inornatus* paratype, with F2 noticeably longer than wide, **E** *E. barberiellus*, with F2 as wide as long, or nearly so, and **F** *E. banksi*, with F2 noticeably longer than wide. Scale bars 0.5 mm.


**Figure 97.** Pseudopygidial area (in dorsal view) of female **A** *E. packeri* paratype (lunate and wider than long), **B** *E. floridensis* (lunate and nearly as long as wide), **C** *E. scutellaris* (lunate and wider than long), **D** *E. basili* paratype (lunate and wider than long), **E** *E. novomexicanus* (lunate and somewhat wider than long), **F** *E. gibbsi* paratype (campanulate and nearly as long as wide), (G) *E. ilicis* (campanulate and nearly as long as wide), (H) *E. zonatus* (campanulate and nearly as long as wide), and (I) *E. australis* (lunate and wider than long). Scale bars 1 mm. The pseudopygidial area is the apical portion of T5 that changes slope from the rest of the tergum and is covered in short, silvery hairs uniform in length (posteromesad the light blue lines).


**Figure 98.** Female **A** *E. pusillus*, ventral habitus, showing color contrast between the dark brown antennae and metasomal sterna and the reddish-orange legs, and **B** *E. basili* paratype, ventral habitus, showing antennae, legs, and metasomal sterna with similar reddish-orange coloration. Scale bars 3 mm.


**Figure 99.** Metasoma (in dorsal view) dampened with water to show differences in integument coloration between T1 of male **A** *E. nebulosus* paratype, which is entirely black, and **B** *E. novomexicanus*, which is red beneath the apical fascia. Scale bars 2 mm. Note that lightly wetting the terga with ethanol allows for this feature to be seen without having to remove the tomentum.

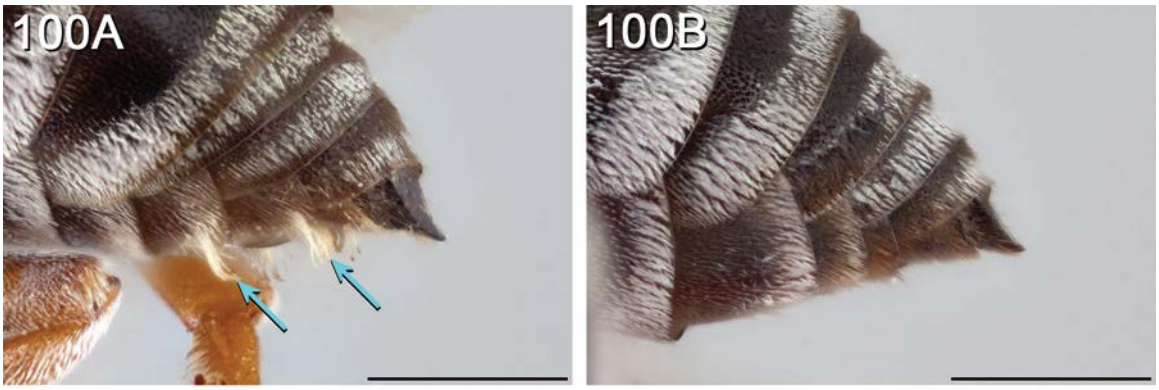


**Figure 100.** Metasoma (in lateral view) of male **A** *E. ilicis* showing long curved subapical hairs on S4 and S5 and **B** *E. inornatus* allotype showing very short straight subapical hairs on the same sterna. Scale bars 1 mm.


**Figure 101.** Mesoscutal pubescence (dorsal view) in males of *E. minimus* **A** as paramedian bands joined apically and **B** entirely obscuring the integument. Scale bars 1 mm.

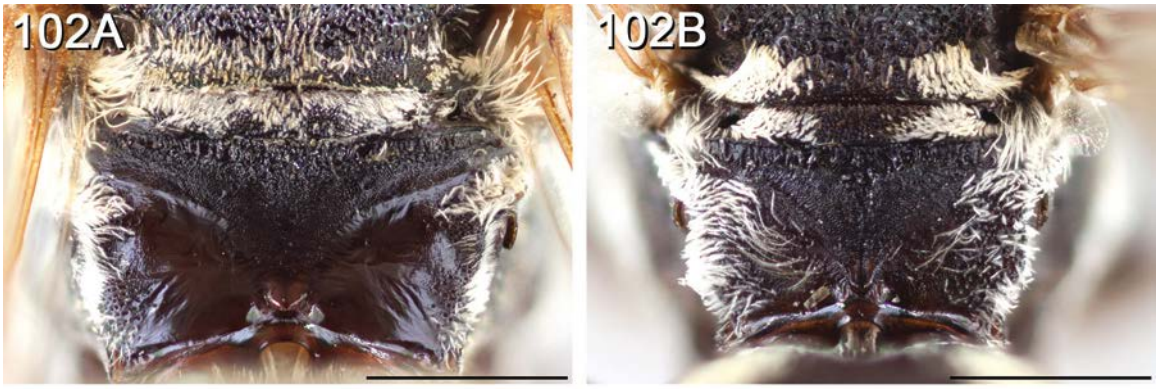


**Figure 102.** Propodeum (in posterior view) of female **A** *E. splendidus* paratype and **B** *E. canadensis*. Scale bars 1 mm.

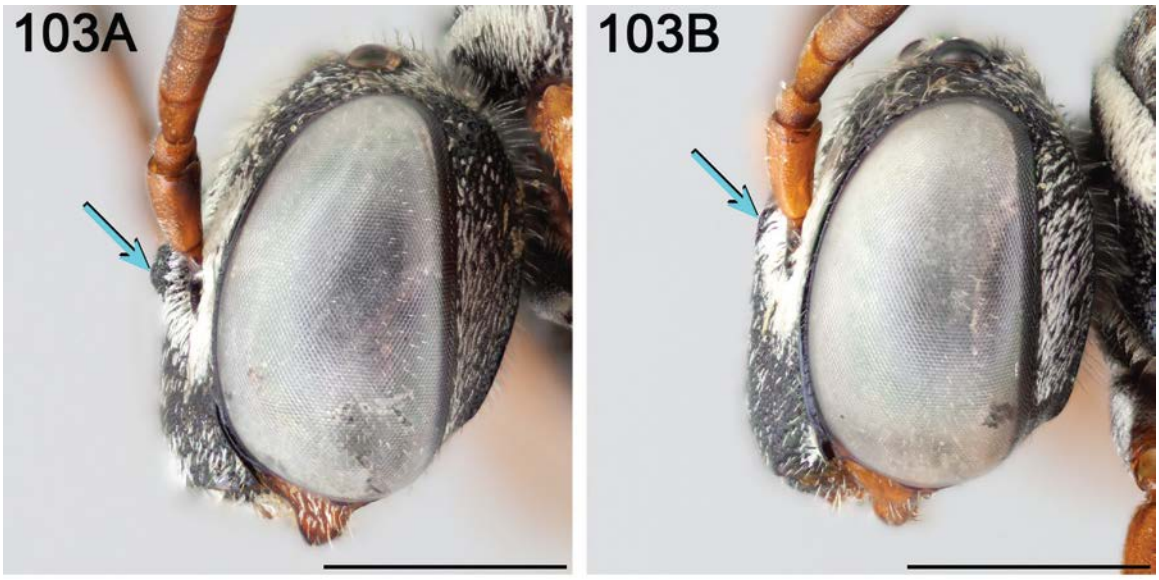


**Figure 103.** Head (in lateral view) of female **A** *E. australis*, in which the frontal keel is strongly raised, and **B** *E. brumleyi* paratype, in which the frontal keel is only weakly protuberant. Scale bars 1 mm. Note that the supraclypeal area is usually covered in dense white tomentum, which was partially removed in these specimens to show the maximum extent of the keel.

**Supplementary material 1**

**Database of *Epeolus* records**

A comprehensive compilation of Nearctic *Epeolus* records used to estimate species ranges, presented for each species as a map showing the known extent of occurrence. Most records are of personally examined specimens, though some are taken from literature or online sources. Specimens used in DNA barcoding include sample processing IDs, barcode index numbers are given for sequences that are BIN-compliant, and GenBank accession numbers are presented for sequenced specimens.

Link: https://doi.org/10.3897/zookeys.755.23939.suppl1

**Supplementary material 2**

**Neighbor-joining tree of DNA barcode sequences**

A Neighbor-Joining tree of 181 Nearctic *Epeolus* COI sequences >300 bp in length (no BINs were assigned to sequences <300 bp in length) based on Kimura's two-parameter distance model, generated in BOLDSYSTEMS (http://www.boldsystems.org) and presented in the

Multipage Classic format. For each sample, the country and province or state in which the specimen that was the source of genetic material was collected is given, as is the processing ID and (if applicable) BIN. Detailed collection information for each sequenced specimen is presented in Suppl. material 1.

Link: https://doi.org/10.3897/zookeys.755.23939.suppl2

**Supplementary material 3**

**Morphological key**

Modifications to the key to species of *Epeolus* in Canada of Onuferko (2017) to include *E. gibbsi*, which has been discovered since from a specimen collected in Manitoba, and *E. inornatus*, which might occur in the country given its presence in New England. The modified key picks up from the second half of couplet 3 in the original key, and unless otherwise stated cites figures published in the present article.

Link: https://doi.org/10.3897/zookeys.755.23939.suppl3

**Chapter 4: Phylogeny and biogeography of the cleptoparasitic bee genus *Epeolus* Latreille (Hymenoptera: Apidae: Nomadinae) and co-speciation with its host bee genus *Colletes* Latreille (Hymenoptera: Colletidae: Colletinae)**

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## Abstract

The bee genus *Epeolus* Latreille (Hymenoptera: Apidae) consists of more than 100 species, which are known to be exclusively cleptoparasites of polyester bees of the genus *Colletes* Latreille (Hymenoptera: Colletidae). Both genera have a nearly cosmopolitan distribution, and are represented on all continents except Antarctica and Australia. The most comprehensive phylogeny for *Epeolus* to date is proposed, based on combined molecular and morphological data. In total, 53 ingroup taxa (species of *Epeolus*) and 7 outgroup taxa (other Epeolini) were scored for 91 morphological characters, and sequence data were obtained for six (one mitochondrial and five nuclear) genes (4,558 bp in total). The crown age of *Epeolus* was estimated to be between 18 and 17 Ma, and its origins were traced to the Holarctic region. Bayesian methods and Maximum Parsimony consistently recovered four distinct intrageneric groups and trees with remarkably similar topologies. The evolutionary history of *Epeolus* is explored in the context of the evolutionary history of its host genus *Colletes*, for which a molecular phylogeny was constructed based on the same genes, and earth history events. A comparison of *Epeolus* and *Colletes* phylogenies limited to taxa for which there is some evidence of an association suggests there was some co-speciation. However, cladogenesis events in *Epeolus* were more frequently linked to instances of dispersal/vicariance. It is not yet clear the extent to which allopatric speciation contributed to diversification in *Colletes*, but the genus'

success in having colonized and diversified across much of the globe made it possible for *Epeolus* to do the same.

**Introduction**

Upwards of 15% of the more than 20,000 described species of bees (Hymenoptera: Apoidea) are cleptoparasitic, at least three times the number of species that exhibit any degree of eusocial behavior (Batra 1984). Whereas the role of eusociality in bee evolution has received a great deal of attention (Danforth 2002, Danforth et al. 2003, Cardinal and Packer 2007, Schwarz et al. 2007, Cardinal and Danforth 2011, Gibbs et al. 2012, Rehan et al. 2012), virtually no studies have attempted to elucidate the evolutionary mechanisms responsible for generating the comparatively large diversity of cleptoparasitic bees. The bee genus *Epeolus* Latreille (Hymenoptera: Apidae: Nomadinae) is an ideal model to study the effects of host evolution and earth history events on bee cleptoparasite diversification. First, insofar as is known, species of *Epeolus* exclusively parasitize a single genus of bees (*Colletes* Latreille [Hymenoptera: Colletidae: Colletinae]) (additional associations suggested by Michener 1974 with *Ancyloscelis* Latreille [Hymenoptera: Apidae: Apinae] and *Melitoma* Lepeletier & Serville [Hymenoptera: Apidae: Apinae] remain uncorroborated). Diagnostic for *Epeolus* is a uniquely-modified female sixth sternum, which consists of a pair of convergent apical lateral processes rigidly attached to a large lobe-like disc. These processes bear setae modified into pointed denticles, which female *Epeolus* spp. presumably use to cut through the cellophane-like lining separating the brood cells and covering the cell walls of their *Colletes* hosts' nests, through which females of *Epeolus* oviposit (Rozen and Favreau 1968, Torchio and Burdick 1988). This morphological specialization on colletids and association with a single host genus makes it possible to identify the likely host species of species of *Epeolus* based on spatial and temporal co-occurrence and other means (e.g. shared chemistry due to odor mimicry of *Colletes* by associated *Epeolus* and/or their association with the same floral communities, Onuferko, in prep.). Known or likely *Epeolus*-*Colletes* cleptoparasite-host associations of Nearctic and Western Palaearctic species are given in Onuferko (2017, 2018) and Bogusch and Hadrava (2018), respectively. Second, *Epeolus* belongs to the exclusively cleptoparasitic apid subfamily Nomadinae, the largest taxon of cleptoparasitic bees (Michener 2007), so factors contributing to the diversification of *Epeolus*

might have also been important in the evolutionary history of other nomadine genera. Third, *Epeolus* exhibits a nearly cosmopolitan distribution. Although *Epeolus* is known to be most diverse in North America (Onuferko 2018), the genus is represented by a large number of species in the Old World, and is the only member of its tribe represented in sub-Saharan Africa and South Asia. Therefore, its evolutionary history can be examined on a global scale in the context of earth history events (i.e. palaeoclimatological, palaeoecological, and palaeogeological phenomena).

Species of *Epeolus* have been described under various supraspecific names, including the following which are all now considered to be junior synonyms (Rightmyer 2004): *Trophocleptria* Holmberg and the monospecific *Diepeolus* Gribodo, *Monoepeolus* Gribodo, *Pyrrhomelecta* Ashmead, *Argyroselenis* Robertson, and *Oxybiastes* Mavromoustakis. Initially a generic name, *Trophocleptria* has since been regarded as a subgenus of *Epeolus* (Michener 2000) and later a synonym by Rightmyer (2004), who found that its placement on a morphological phylogeny rendered *Epeolus* (*Epeolus*) paraphyletic. For *Trophocleptria* to retain its subgeneric status, the rest of *Epeolus* would have to be divided into various subgenera, but other distinct groupings have not yet been identified. However, the taxon appears to be monophyletic, and Michener (2007) suggested that the name "Trophocleptria group" be used.

The present study aims to address the following objectives: 1) to construct the most comprehensive phylogeny of the bee genus *Epeolus* to date in a total evidence approach (*sensu* Kluge 1989); 2) to test the validity of previous classifications adopted for members of the genus (and to provide any updates if necessary); and 3) to elucidate the effects of host diversification (by comparing dated phylogenies of *Epeolus* and *Colletes*) and biogeographic factors on *Epeolus* speciation.

## Materials and methods

### Taxon and Gene Sampling (Tables S1 & S2)

All species of Epeolini represented in the apid molecular phylogeny published by Cardinal et al. (2010) were included in the present study and were originally identified as follows: *Doeringiella* Holmberg sp., *Epeolus* Latreille sp., *E. scutellaris* Say, *E. variegatus*

(Linnaeus), *Odyneropsis* Schrottky sp., *Rhinepeolus rufiventris* (Friese), *Thalestria spinosa* (Fabricius), and *Triepeolus robustus* (Cresson). Specimen details and voucher numbers are given in Table S1 of Cardinal et al. (2010), and GenBank accession numbers are given in Table S2 of the present publication. Specimens of the following three taxa were examined: *Doeringiella* sp., which in the present study has been identified as *Doeringiella* cf. *holmbergi* (Schrottky) using Roig-Alsina's (1989) key, *Epeolus* sp., which in the present study has been identified as *E. variolosus* (Holmberg), and *Rhinepeolus rufiventris*. All three are at the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC) in Ottawa, Ontario, Canada. The vouchers of *Thalestria spinosa* and *Triepeolus robustus* were not examined, but the species are easily diagnosable and unlikely to have been misidentified. The remaining vouchers could not be traced. It is unclear with which species or even subgenus of *Odyneropsis* the only nuclear ribosomal and protein-coding gene sequences available are associated. Unfortunately, the source specimen (according to B.N. Danforth) was completely destroyed in the DNA extraction process (S. Bossert, personal communication). The single nuclear protein-coding gene sequence available for *E. schummeli* Schilling (on GenBank) from a study by Gerth et al. (2013) (see Table S2 for accession number) was also included.

Additional specimens used in obtaining nuclear ribosomal and protein-coding gene sequences were collected by TO, RF, LP, and the external collaborators named in the Acknowledgements (see Table S2 for specimen collection and vouchering details). The number of unique taxa for which these data were included is 25, of which two are species of *Triepeolus* and 23 are species of *Epeolus*. The species of *Triepeolus* are *T. pectoralis* (Robertson) (from North America) and *T. tristis* (Smith) (one of only two species in the genus known from the Old World). Among the species of *Epeolus*, 18 are from North America, 4 are Eurasian, and 1 is South African.

To add to the molecular data, mitochondrial DNA sequences from a segment of the cytochrome c oxidase subunit 1 (COI) gene (DNA barcode region, Hebert et al. 2003a, b) were included for most of the abovementioned taxa and 26 additional *Epeolus* species (23 from North America, one from North Africa, and one from South Africa). Most barcode sequences were previously published (Onuferko 2018), but those associated with the outgroup taxa and *Epeolus* spp. that do not occur in North America are new. These and other new sequences (see Tables S1 & S2 for voucher numbers) will be made available in GenBank

(https://www.ncbi.nlm.nih.gov/genbank/) upon publication of this manuscript. In total, 60 taxa were included in phylogenetic analyses, of which 7 are outgroup taxa and 53 are ingroup taxa (*Epeolus* spp.). Altogether, of the sampled *Epeolus* spp. three are from Africa, six occur in Asia and/or Europe, 43 are from North America, and one is from South America.

To explain the evolutionary history of *Epeolus* in the context of that of its host genus, a dated *Colletes* phylogeny was constructed that includes two outgroup taxa, *Callomelitta antipodes* (Smith) (a non-colletine colletid, which was selected as the root) and *Hemicotelles ruizii* (Herbst), a colletine which Almeida et al. (2009, 2012) found to be sister to *Colletes*, and 18 ingroup taxa (species of *Colletes* that are known or presumed to be hosts of species of *Epeolus*). The analysis was limited to species of *Epeolus* and *Colletes* for which cleptoparasite-host associations are known or have been proposed and for which sequence data are available. Sequence and specimen voucher details (for *Colletes* and *Epeolus*) are indicated in Table S1.

Tissue and DNA Extraction Protocol

Field collected specimens were killed in >95% ethanol (or >95% isopropanol if ethanol was unavailable, in which case the specimens were later transferred to vials containing 100% ethanol), and stored in glass vials between -10°C and -20°C. For tissue removal, the head, prosternum, propleura, and forelegs were detached, exposing the muscle tissue within the mesosoma, which was removed with fine-tipped forceps that were sterilized beforehand by flame and rinsed in 100% ethanol. The mostly hollow specimens were then pinned with the head and forelegs glued back (for vouchering purposes) with water-soluble clear Elmer's glue (Made in China ©2015 Elmer's Products, Inc). In most cases, a few legs were also taken (for in-house extraction and/or to be sent to the Canadian Centre for DNA Barcoding in Guelph, Ontario, Canada), usually the mid and hind legs on the specimen's right side so that one side was intact. Tissues were placed in Eppendorf tubes, which were immersed in liquid nitrogen for a few seconds, and subsequently ground with blue polypropylene pellet pestles. DNA was extracted using the Mag-Bind® Blood DNA HDQ 96 Kit (Omega Bio-tek, Inc.). Some of the reagents required additional preparation: dilution with 100% ethanol or 100% isopropanol (detailed protocols are given in the product manual). For lysis, 350 µL of TL buffer and 20 µL of Proteinase K Solution were added to each Eppendorf tube, which was vortexed for about 10

seconds and placed in an incubator overnight set to 50°C. The next day the tubes were vortexed for 10 minutes before the lysate was transferred to sterile tubes, which were vortexed for another 10 minutes. Finally, 250 μL of lysate was transferred to a 96-well Thermo Scientific microtiter deep well plate. To each well, 290 μL of AL Buffer, 400 μL of HDQ Binding Buffer, and 20 μL of Mag-Bind® Particles HDQ were added. The following reagents were transferred to a series of separate microtiter deep well plates (one per reagent) with the volume corresponding to each sample given in parentheses: VHB Buffer (two plates, each used well filled with 600 μL), SPM Wash Buffer (600 μL), and nuclease-free water (500 μL). The Elution Buffer was transferred to a KingFisher 96 KF plate (Thermo Fisher Scientific) (100 μL/sample). The plates as well as one KingFisher 96 KF plate Tip Pick Up were placed inside a KingFisher Flex Magnetic Particle Processor with 96 Deep Well Head, and the automated extraction was performed using Thermo Scientific BindIt 3.3.1 Software. The purified DNA was transferred to sterile Eppendorf tubes and stored at -20°C.

Gene Selection, Amplification, and Sequencing

Most of the genes upon which Cardinal's (2010) comprehensive phylogeny of Apidae was based were selected for the present study. This allowed for a mixture of rapidly-evolving and slowly-evolving genes to help resolve deep-level and shallow-level relationships. The molecular dataset consists of sequences of one mitochondrial gene (COI), one nuclear ribosomal gene (28S), and four nuclear protein-coding genes (EF-1α, long-wavelength rhodopsin [opsin], pol II, and wingless). All COI sequences were obtained through the Biodiversity Institute of Ontario at the University of Guelph in Guelph, Ontario Canada, where DNA was extracted (usually from a midleg from the specimen's right side), the barcode region was amplified using a variety of different primers for different samples, and sequencing (mostly Sanger but in some cases NextGen) and sequence cleanup took place. Barcode records are in the "Phylogeny of North American Colletes" and "Epeolus phylogeny" projects in BOLD (http://www.barcodinglife.org), where for each sample a report is available detailing the molecular procedure that was followed. The remaining genes were amplified at York University using the following primer pairs (purchased from Integrated DNA Technologies) and PCR conditions:

- 28S: Bel28S-For (Belshaw and Quicke 1997) and 28SD4-Rev (Danforth et al. 2006a): 94°C for 1 minute, 56–58°C for 1 minute, and 72°C for 1.5 minutes (35 cycles).
- EF-1α: EmphF2For (Sipes and Wolf 2001) and EmphF2Rev (Sipes and Wolf 2001): 94°C for 1 minute, 54°C for 1 minute, and 72°C for 1.5 minutes (35 cycles).
- Opsin: Opsin-For3(mod) (Almeida and Danforth 2009) and Opsin-Rev(mod) (Almeida and Danforth 2009): 94°C for 1 minute, 57°C for 1 minute, and 72°C for 1 minute (35 cycles).
- Pol II: polfor2a (Danforth et al. 2006a) and polrev2a (Danforth et al. 2006a): 94°C for 1 minute, 55–57°C for 1 minute, and 72°C for 1 minute (35 cycles).
- Wingless: Wg-Collet-For (Almeida and Danforth 2009) and Lep-Wg2a-Rev (Brower and DeSalle 1998): 94°C for 1 minute, 55°C for 1 minute, and 72°C for 1 minute (35 cycles).

*Colletes* sequences were obtained using the same primers and PCR conditions as above except as follows. A different set of primers was used to amplify EF-1α. Opsin amplicons were obtained using one of two primers: the aforementioned pair (with the same PCR conditions) or the one below.

- EF-1α: HaF2For1 (Danforth et al. 1999) and F2-rev1 (Danforth et al. 1999): 94°C for 1 minute, 54°C for 1 minute, and 72°C for 1.5 minutes (35 cycles).
- Opsin: Opsin-For (Mardulyn and Whitfield 1999) and Opsin-Rev (Mardulyn and Whitfield 1999): 94°C for 1 minute, 54°C for 1 minute, and 72°C for 1 minute (35 cycles).

Primers were initially dissolved in TE buffer (100 μM), and aliquots were diluted to 10 μM in autoclaved double-distilled water (dd$H_2O$) for PCR. The reaction mixture for each sample consisted of 28.5 μL of Taq 2X Master Mix, 2.9 μL of the forward primer, 2.9 μL of the reverse primer, 22.7 μL of dd$H_2O$, and 3 μL of purified DNA in Elution Buffer (total volume = 60 μL). Band size and purity of the PCR products were gauged for each sample following gel electrophoresis. Crude PCR products were subsequently sent to Bio Basic Inc. (20 Konrad Crescent, Markham, Ontario, Canada) for purification and Sanger sequencing.

## Data Assembly and Preparation for Phylogenetic Analysis

### Data – Molecular

Using the bioinformatics software platform Geneious 11.1.2 (Kearse et al. 2012), sequences were assembled, trimmed, checked for a) quality, which included replacing questionable designations with nucleotide ambiguity codes, and b) to ensure that no stop codons were present in the coding regions of the nuclear protein-coding genes, and aligned separately for each gene using the ClustalW multiple-alignment algorithm (Chenna et al. 2003). Since sequences of a particular gene differed in length among samples, longer sequences were trimmed. Specifically, regions present in fewer than half of the species with sequences were excluded from the dataset. Both EF-1α and Opsin have non-coding regions, but no introns were removed since the two sets of sequences could all be aligned unambiguously. Six matrices (one per gene) of aligned sequences were individually exported from Geneious as NEXUS files, and using SequenceMatrix (Vaidya et al. 2011) concatenated into a single matrix with 4,558 characters and 59 taxa, which was saved as a NEXUS file. From Mesquite 3.40 (Maddison and Maddison 2018) the file was exported for PartitionFinder (Lanfear et al. 2012) to determine the best model of nucleotide substitution for each gene. The model chosen was based on its intended use for phylogenetic analysis in MrBayes 3.2.6 (Ronquist et al. 2012) (to ensure that only models implemented in MrBayes were considered), model quality was assessed according to the Akaike information criterion (AIC) (Akaike 1974), the 'greedy' algorithm was used to search for a good partitioning scheme (the recommended choice for the size of the molecular dataset, Lanfear et al. 2012), and variation in mutation rate as a result of codon position was taken into account as differences among the three nucleotides of a codon were expected, at least for mitochondrial DNA (Rehan et al. 2010). The dataset was partitioned according to the best model of DNA evolution based on analyses performed with PartitionFinder (a python file), which was executed from the Command Prompt given the concatenated matrix (a PHY file), and a partition finder CFG file containing the command code. Three partitions were identified, and based on the results the following nucleotide substitution rate models were implemented: Propinv for the first partition, Gamma for the second partition, and Invgamma for the third partition. The General

Time Reversible (GTR) model with six substitution types (nst = 6) was applied to each molecular partition. Parameters were unlinked across partitions, so that each had its own set of parameters, and allowed to evolve under different rates using the ratepr parameter of the prest command (Ronquist et al. 2012).

## Data – Morphological

A matrix of 91 morphological characters scored for 60 (7 outgroup and 53 ingroup) taxa was added to the dataset of molecular sequences as an additional, numerical partition. For this fourth partition, the default model settings were implemented, with "coding" set to "variable". Although the morphological dataset is outweighed considerably by the molecular dataset, morphological data were incorporated into all phylogenetic analyses with the expectation that their inclusion would result in the more accurate placement of taxa for which only some sequence data are available and to determine which synapomorphies support particular clades based upon total evidence (Kluge 1989). Morphological characters are new or taken from Rightmyer (2004) (with some modifications) if they were found to vary among the species of Epeolini included in the present study. Given the sizeable number of species of *Epeolus* known from a small number of specimens, characters were limited to features that did not require specimens to be dissected. Autapomorphic character states were avoided and included only if it was impossible to score a species as exhibiting one of the alternative character states shared by at least two taxa. The list of characters and illustrations of each character state are presented in Appendix I and II, respectively. Table S3 in Appendix II shows the complete morphological character matrix.

## Phylogenetic Analysis

### *Epeolus*

In all analyses, the root was set to *Odyneropsis* since published morphological (Rightmyer 2004) and molecular (Cardinal et al. 2010) phylogenies strongly and independently support its status as sister to the rest of Epeolini (in the case of the latter with a posterior

probability of 100%). A BIN-compliant 658 bp sequence is available for an unidentified species of *Odyneropsis* (*Parammobates* Friese), so its sequence data were included, and it and other specimens of the subgenus *Parammobates* were scored for morphology.

## Bayesian Inference (BI)

Bayesian analysis of the combined molecular and morphological data was carried out in MrBayes. Two independent sets of four Markov chain Monte Carlo (MCMC) simulations were run simultaneously, each for 10,000,000 generations, by which point the average standard deviation of split frequencies was below 0.01. Tracer v1.6 (Rambaut et al. 2014) was used assess convergence of both sets of runs and the stationarity of each parameter. The first 25% of the sampled trees were discarded as burn-in. Clade support was expressed as posterior probability values (i.e. frequency values indicating the proportion of sampled trees [drawn from the stationary distribution of the chain] in which a clade appears). Trees were visualized and edited in FigTree v1.4.3 (Rambaut 2016).

## Divergence Dating

An uncorrelated relaxed molecular clock model (Drummond et al. 2006) implemented in the software platform BEAST 2 (Bouckaert et al. 2014) was used to produce dated phylogenies. PartitionFinder was again used to find the best model of DNA evolution but specifically for phylogenetic analysis in BEAST 2. The partitions were the same as those identified for use in MrBayes except that the substitution rate model TRN+I was suggested for the first partition instead of GTR+I (Propinv). The concatenated sequence matrix was imported into BEAUti 2 (Bouckaert et al. 2014), and the morphological character set partition was added separately using the accompanying package MM. Since no DNA sequences are available for *Epeolus banksi* (Cockerell), the species had to be excluded from the dating analysis to allow for the linking of Clock Models and Trees across partitions, for which identical sets of taxa are required. This step ensures that the partitions share the same evolutionary history. Site models, however, were unlinked to allow for the molecular partitions to have their own relative rates of nucleotide substitution. For the morphological partition, the Lewis Mk model (Lewis 2001) was specified,

which allows for the transition of any state to any other state and treats all transitions as equally probable.

The calibrated Yule model, which the BEAST 2 divergence dating tutorial (Drummond et al. 2015) recommends for analyses using sequences from different species, was selected as the tree prior. To date, only one fossil of a presumably cleptoparasitic bee, *Paleoepeolus micheneri* Dehon et al., is known, and phylogenetic analysis based on geometric morphometrics of the fore wing shape placed it within a clade of cleptoparasitic apids that includes the subfamily Nomadinae and tribe Melectini (Dehon et al. 2017). The fossil bee is Palaeocene (c. 60 Ma), and older than the crown age estimated for Epeolini (c. 44 Ma) by Cardinal et al. (2010). In the absence of Epeolini fossils, a single calibration point derived from the comprehensive dated apid phylogeny of Cardinal et al. (2010), which incorporated fossil data of non-parasitic apids to calibrate 10 internal nodes, was used in the present study. Specifically, a lognormal distribution with a lognormal mean of 3.5 (33 Mya) and SD of 0.1 was applied to the node uniting the members of the subtribes Epeolina Robertson and Thalestriina Rightmyer, which is sister to Odyneropsina Handlirsch (the root in the present study).

Having generated the BEAST XML file, an analysis was run for 50,000,000 generations. Subsequent analyses were run to see if the topology stayed the same when the data were reanalyzed. Trace files for all parameters were examined using Tracer. Having discarded the appropriate burn-in (identified through Tracer as the first 5 million generations [10%]), posterior trees were summarized using the program TreeAnnotator (available as part of the BEAST package) to get the maximum clade credibility tree. The lower proportion (but higher number) of samples discarded to calculate the BEAST tree is explained by the difference in the number of generations for which analyses were run between MrBayes and BEAST 2 and how many it took to reach stationarity.

*Colletes*

Except as follows, the same procedure used to produce a dated phylogeny for *Epeolus* was used to construct one for *Colletes*. The dataset was comprised entirely of nucleotide sequences (morphology was not assessed). Whereas all other sequences were aligned with ClustalW, Opsin sequences of *Colletes* had to be aligned using the MAFFT multiple alignment

algorithm (Katoh et al. 2002) to correct for differences in sequence direction (some sequences were assembled backwards). PartitionFinder identified five partitions, and based on the results the following nucleotide substitution rate models were implemented: GTR+G for the first partition, TrN+G for the second partition, GTR+I+G for the third partition, TrN+I+G for the fourth partition, and HKY+G for the fifth partition. A single node was calibrated. Given the taxa included in the phylogeny, it was not possible to calibrate it with fossils. Only two fossils of colletid bees are known, and both are rather recent in age, belonging to the extant genus *Chilicola* Spinola (subgenus *Hylaeosoma* Ashmead) in the subfamily Xeromelissinae (Michener and Poinar 1996, Engel 1999, Miklasevskaja 2017). Instead, we referred to the comprehensive colletid phylogeny of Almeida et al. (2012) for approximate node ages, which were obtained through their implementation of a relaxed molecular clock model. Based on this phylogeny, a lognormal distribution with a lognormal mean of" 3.4 (30 Mya) and SD of 0.1 was applied to the node uniting *Colletes* and *Hemicotelles ruizii* (Herbst).

Maximum Parsimony (*Epeolus* only)

To determine if similar topologies can be recovered independently by different means from the same dataset, thereby assessing its robustness, maximum parsimony (MP) analyses were performed in TNT 1.1 (Goloboff et al. 2008). Uninformative molecular characters were mopped in WinClada 1.00.08 (Nixon 2002) and removed from the dataset prior to its use in MP analysis. The final dataset was comprised of 700 (91 morphological and 609 molecular) informative characters.

Having set aside space for 10,000 trees in memory, "New Technology" algorithms implementing the Parsimony Ratchet (Nixon 1999), Tree Drifting (Goloboff 1999), and Tree Fusion (Goloboff 1999) were used to search for trees, with the random seed set to 0 and 5 initial sequences added (the default setting), until the minimum length was found 1,000 times. Constraints for monophyly were enforced for all species pairs that share a BIN (i.e. barcode sequences from a given pair of species were similar enough to be assigned the same unique barcode identifier number, which usually corresponds to a single species (Ratnasingham and Hebert 2007, 2013)). The pairs are *E. americanus* (Cresson) and *E. barberiellus* Cockerell, *E. glabratus* Cresson and *E. lectoides* Robertson, *E. ilicis* Mitchell and *E. zonatus* Smith, *E.*

*novomexicanus* Cockerell and *E. pusillus* Cresson, and *E. packeri* Onuferko and *E. scutellaris* Say, all of which are considered to be sister species pairs (Onuferko 2018). Subsequently, implied weighting analysis (Goloboff 1993, Goloboff et al. 2008, Goloboff 2014) with weights chosen by using the script 'setk.run', written by Dr. J. Salvador Arias (Instituto Miguel Lillo, San Miguel de Tucumán, Argentina) (its use published in Santos et al. 2015), was used. The purpose was to see if a more resolved tree could be obtained when a defined concavity weighting factor (k) is used to downweight characters that exhibit multiple state changes on a tree, with lower values of k corresponding to a higher penalty for homoplasy. Branch support was determined by symmetric resampling (Goloboff et al. 2005) with 10,000 replicates, with the output given as GC values (frequency differences between a group and the most frequent contradictory group). Unlike other methods, which produce over- or underestimations of group support when character weights are changed (as under implied weighting), symmetric resampling is not affected by character weight and transformation costs (Goloboff et al. 2005).

The tree file produced in TNT was opened in WinClada in conjunction with just the morphological character matrix. The characters and corresponding states were mapped onto the single most parsimonious (or consensus) tree to show which synapomorphies supported which clades.

## Comparison of Host and Cleptoparasite Phylogenies

Associations between North American species of *Colletes* and *Epeolus* are taken from Onuferko (2017, 2018), wherein previously reported associations are reviewed and new ones are proposed. It should be noted that most of these come from observations of spatial and temporal co-occurrence in the field, and that associations based on nest excavations are extremely rare due to the difficulty of locating *Colletes* nests, let alone the fraction that have been parasitized. In North America, only *E. compactus* Cresson, *E. ilicis*, and *E. pusillus* have been associated with their host species this way. Some species of *Epeolus* are so rarely collected that information about their hosts will likely not be available for some time. As a result, comparisons of *Epeolus* and *Colletes* phylogenies are limited to the taxa for which there is some evidence of an association (be it definitive or circumstantial), and herein cophylogenetic analyses are focused on 18 species of *Colletes* and 18 species of *Epeolus* (15 Nearctic and three Palaearctic species

pairs). The Palaearctic associations are as follows: *E. tarsalis* Morawitz with *C. collaris* Dours and *C. halophilus* Verhoeff (Pittioni 1945, Peeters et al. 1999), and *E. schummeli* Schilling with *C. nasutus* Smith (Celary 1990, Westrich 1990).

Comparisons of the evolutionary history of hosts and cleptoparasites were tested in two ways. First, a test of independence was performed using the program ParaFit (Legendre et al. 2002), which tests the null hypothesis that the evolution of two groups of organisms has been independent given their associations and phylogenies. As input, the program requires a matrix of links between hosts and parasites as well as principal coordinates (in this case obtained with the program DistPCoA, Legendre and Anderson 1998) derived from distance matrices for hosts and parasites. For PCA, patristic distances associated with the dated maximum clade credibility trees from BEAST were used. Second, the software platform Jane 4 (Conow et al. 2010) was used to reconstruct the historical events that best explain associations between extant species of *Epeolus* and *Colletes*. The program uses a cost structure, which can be manipulated, and by default co-speciation is considered to be the most parsimonious hypothesis and assigned a cost of 0. This is because for co-speciation to occur only divergence is required, whereas all other scenarios (duplication, host switching, sorting events [parasite loss by extinction or "missing the boat"], and failure to diverge) require at least one extra step, and are by default assigned a higher cost (de Vienne et al. 2013). In the present analysis, the default cost structure was used and the results were compared to those of a manipulated cost structure (the effects of assigning a high cost to each event type relative to others on reconciliation were compared, as in Althoff et al. 2011) to see if changing it resulted in alternative explanations regarding the evolutionary history of the compared clades. For each analysis, both the number of generations (i.e. iterations of the algorithm) and population size (i.e. the number of samples per generation) were set to 1,000. ParaFit and Jane were used because both methods allow for more than 1:1 correspondence between host and parasite tips and make use of dated phylogenies. In Jane, this is done by moving nodes into specific time zones on a scale that is set by the user. Doing so ensures that co-speciation is inferred only whenever there is both topological and temporal congruence between clades. In the present study, nodes were positioned into one of 7 time zones based on the results of the dating analysis in BEAST 2 (see Biogeography section under Results below), and a node in the *Epeolus* tree can only be mapped to a region of the *Colletes* tree in the same time zone. Since the program requires a host node to be present in each time zone, some time zones

represented longer periods of time than others (4 million as opposed to 2 million years). Hence, time zones (from the oldest to current) were specified as follows: 1 = 20–16 Mya, 2 = 16–14 Mya, 3 = 14–12 Mya, 4 = 12–8 Mya, 5 = 8–4 Mya, 6 = 4–2 Mya, and 7 = 2 Mya to present time.

## Biogeography

Two approaches were taken to study the evolution of *Epeolus* in a historical biogeographic context. First, probabilistic ancestral ranges at each node were estimated using the package BioGeoBEARS (Matzke 2013) installed in R (version 3.3.2) (R Core Team 2016), which uses the likelihood-based dispersal-extinction-cladogenesis (DEC) model of Ree and Smith (2008). As input, the dated phylogeny from BEAST was used. Five areas were considered in the implemented model: the Afrotropic (AF), the Florida peninsula and coastal Georgia (an area with multiple endemic species of *Epeolus*, Onuferko 2018) (FL), the Nearctic (including the Florida panhandle) (NA), the Neotropic (excluding the Florida peninsula) (NT), and the Palaearctic (PA). The maximum range size was set to include all five areas. Second, to infer whether or not cladogenesis events were the result of allopatric speciation, a spatial analysis of vicariance was carried out using the Vicariance Inference Program (VIP) of Arias et al. (2011). Unlike other methods in historical biogeography, VIP, which is based on the ideas of Hovenkamp (1997, 2001), uses actual distribution data, and takes as input a phylogenetic tree and GPS coordinates associated with species occurrence records (Arias et al. 2011). It then decides on which geographic disjunctions best explain the mapping of coordinates onto the phylogeny. A tree file was written manually to reconstruct the topology of the phylogeny obtained through BEAST, but without specifying branch length, which VIP does not consider, and to include *E. banksi*, which could not be included in a dated phylogeny due to a lack of DNA sequence data. In conjunction with the MP data matrix, the tree was opened in TNT and converted to an XML file using the macro ‘toxml.run’. Occurrence records for most species were taken from the exhaustive lists of examined material presented in Bogusch and Hadrava (2018) and Onuferko (2018) (Supplementary material 1). For other species and representatives of Palaearctic species occurring in Asia, which are not included in the revision by Bogusch and Hadrava (2018), records were compiled based on material examined by TO and PB (Table S1) and from Discover Life (Ascher and Pickering 2018) if the data were associated with species

unlikely to have been misidentified. Distributional data were not included for the outgroup taxa, for which taxon sampling was too limited for any inferred instances of dispersal/vicariance between sister groups to be meaningful. For the analysis, a grid size of 0.5° × 0.5° was used (given the dataset, this corresponds to a latitude length of 55.3–55.8 km and longitude length of 23.0–53.9 km). The maximum fill was set to 1 (this extends the area of occupancy to the eight cells immediately surrounding the cell in which the actual record falls [Moore neighborhood, Weisstein 2005]). The maximum amount of range overlap allowed between two species was set to 25% (as in Monckton 2016) to account for the possibility that in some cases barriers disappeared following divergence, allowing sister species to partially extent their ranges into areas occupied by the other. Following Monckton (2016) and Postlethwaite (2016), the cost of distribution removal was increased (to 5) from the default number (1), which may overestimate the number of dispersal/vicariance events since a lower cost allows for the more liberal removal of distributions of widespread taxa if it increases the number of disjoint distributions (Arias et al. 2011). A lower cost allows for back-dispersal into an area, and leads to more inferences of disjunctions at internal nodes (Postlethwaite 2016). For the remaining parameters the default settings were used, and a Heuristic search was conducted with 1,000 iterations.

## Results

### *Epeolus* phylogeny

Phylogenies obtained through Bayesian methods indicate strong support for the monophyly of *Epeolus*, with a posterior probability of 100%. Through dating analysis in BEAST 2, the crown age of *Epeolus* was estimated to be between 18 and 17 Ma. The timing of divergence events within *Epeolus* did not change very much upon selecting a different calibration point; an alternative analysis was run in which a lognormal distribution with a lognormal mean of 3.0 (20 Mya) and SD of 0.1 was applied to the node uniting *Doeringiella* cf. *holmbergi* and *Rhinepeolus rufiventris* (in both Cardinal et al. 2010 and in the present study, the two taxa came out as sister to one another). With the alternative analysis, a more recent crown age for *Epeolus* was inferred (c. 15 Ma), whereas the ages of all other ingroup nodes differed by less than 2 million years between the two trees. The tree obtained with the original calibration

point is preferred here because setting the age of the node uniting Epeolina and Thalestriina to 33 Ma gave an estimated age of about 20 Ma anyway to the node uniting *Doeringiella* and *Rhinepeolus*, whereas calibrating the latter node to 20 Ma resulted in a much more recent estimate of divergence for the sister taxon to Odyneropsina (c. 24 Ma). Additionally, the crown ages of both Epeolini and *Epeolus* are much closer to the estimates obtained for those groups by Cardinal et al. (2010) when the original calibration point was used. The topologies of the trees obtained through MrBayes and BEAST 2 are for the most part congruent (Figs. 1 & S1). However, whereas the dated phylogeny includes nodes with a posterior probability of less than 50%, in the undated phylogeny phylogenetic uncertainty is indicated by a total of five polytomies because nodes with <50% support are collapsed.

Two equally parsimonious trees were recovered by MP analysis on the combined dataset in which characters were weighted equally (length: 3,054; CI [consistency index]: 0.346; and RI [retention index]: 0.553). With implied weighting (k = 10 [the estimated value]), a single tree was recovered (length: 3,060; CI: 0.346; and RI: 0.553) (Fig. 2), which was topologically almost identical to the consensus tree based on equally weighted characters. The only differences are as follows. In the equally weighted tree, *E. australis* Mitchell came out as sister to *E. brumleyi* Onuferko. Additionally, *E. andriyi* Onuferko came out as sister to the remaining 22 species in its clade, and the clade that includes *E. carolinus* Mitchell and *E. rufulus* Cockerell came out as sister to the clade that includes *E. glabratus*, *E. lectus* Cresson, and *E. lectoides*. Finally, the positions of *E. erigeronis* Mitchell and *E. inornatus* Onuferko switched between the two most parsimonious trees based on equally weighted characters, resulting in a polytomy. Symmetric resampling gave strong support for the monophyly of *Epeolus* (branch support = 99%).

Both BI and MP analyses using the combined molecular and morphological datasets yielded phylogenies with remarkably similar topologies, with each recovering four major groupings of species. Included is a Nearctic/Neotropical clade (group A) comprised almost entirely of species in which the axilla is short (with its tip extending to less than 2/3 the length of mesoscutellum [maximum posterior extent is shown in Onuferko 2018, Fig. 20D]) and small. There is a second Nearctic/Neotropical clade (group B) that includes *E. interruptus* Robertson, *E. tessieris* Onuferko, and species in the “Trophocleptria group”, in which some species at least have a sparsely punctate mesopleuron and/or a blunt median process on the metanotum (Onuferko 2018, Fig. 61D), and lack the fleshy lateral lobes of the penis that are present in males

of most *Epeolus* spp. (Rightmyer 2004, Figs. 141 & 142). A third Old World clade (group C) is comprised of African and Eurasian species, most of which have medially rather than apically positioned tubercles on the labrum (Fig. S3B), exhibit sexual color dimorphism with regard to the axilla and mesoscutellum (e.g. Bogusch and Hadrava 2018, Figs. 23 & 24), and have similar patterns of pubescence on the metasomal terga. Lastly, there is a Nearctic clade (group D) comprised of species in which the axilla is long (with its tip extending to or beyond 2/3 the length of the mesoscutellum [minimum posterior extent is shown in Onuferko 2018, Fig. 12D]) and arcuate, conspicuously diverging from the side of the mesoscutellum (its free portion is ~2/5 its entire medial length or longer, Onuferko 2018, Fig. 53D), or both. Within group D there is a monophyletic group in which the axilla is distinctly hooked and the pseudopygidial area of the female T5 is distinctly campanulate (i.e. bell-shaped) (Onuferko 2018, Fig. 97F–H); in all other species of *Epeolus* it is lunate (i.e. semicircular) (Onuferko 2018, Fig. 97A–E & I). Many of the same minor clades in the preferred (dated) tree from BEAST were also present in the TNT tree and were strongly supported. Although all phylogenies are largely very similar, there are two species whose relationship to other species of *Epeolus* differs dramatically among the various topologies: *E. flavociliatus* Friese and *E. transitorius* Eversmann. Both are Old World species and exhibit certain peculiarities. Morphologically, *E. flavociliatus*, whose range extends across North Africa and the Middle East, shares many features with various species in the exclusively Nearctic clade (group D), namely the distinctly elongate and hooked axillae and presence of a pair of tubercles on the apical margin of the labrum. Independent analyses in BEAST 2 gave conflicting results, placing *E. flavociliatus* either as sister to the rest of *Epeolus* or within group D. Since independent analyses in MrBayes and TNT consistently produced topologies consistent with the former scenario, the preferred BEAST tree is the one that shows *E. flavociliatus* to be sister to the rest of the genus. Branch support for group D increased to 100% when *E. flavociliatus* was excluded from phylogenetic analysis in BEAST 2, and the composition of species in groups B, C, and D did not change upon its removal. The only major differences were as follows: the clade that includes *E. australis*, *E. brumleyi*, and *E. flavofasciatus* came out as sister to the rest of *Epeolus*, and the clade that includes *E. chamaesarachae* Onuferko and *E. diadematus* Onuferko came out as sister to the Old World clade. When all data were considered, support for the inclusion of both clades in group A was high (79%). *Epeolus transitorius* is also unusual among Old World species as it too has a pair of tubercles on the apical margin of the

labrum. Analyses place it either within the Nearctic/Neotropical clade almost entirely comprised of species in which the axilla is short (group A) or within the Old World clade (as sister to the other African and Eurasian species) (Fig. 2). Although branch support for each of the four major groupings within *Epeolus* was comparatively weak in the MP phylogeny, it is notable that these groups were comprised of the same species (with the exception of *E. transitorius*) in both BI and MP trees and that their topologies are remarkably congruent. Also notable is that topology of the outgroup taxa is identical between the BEAST and TNT phylogenies.

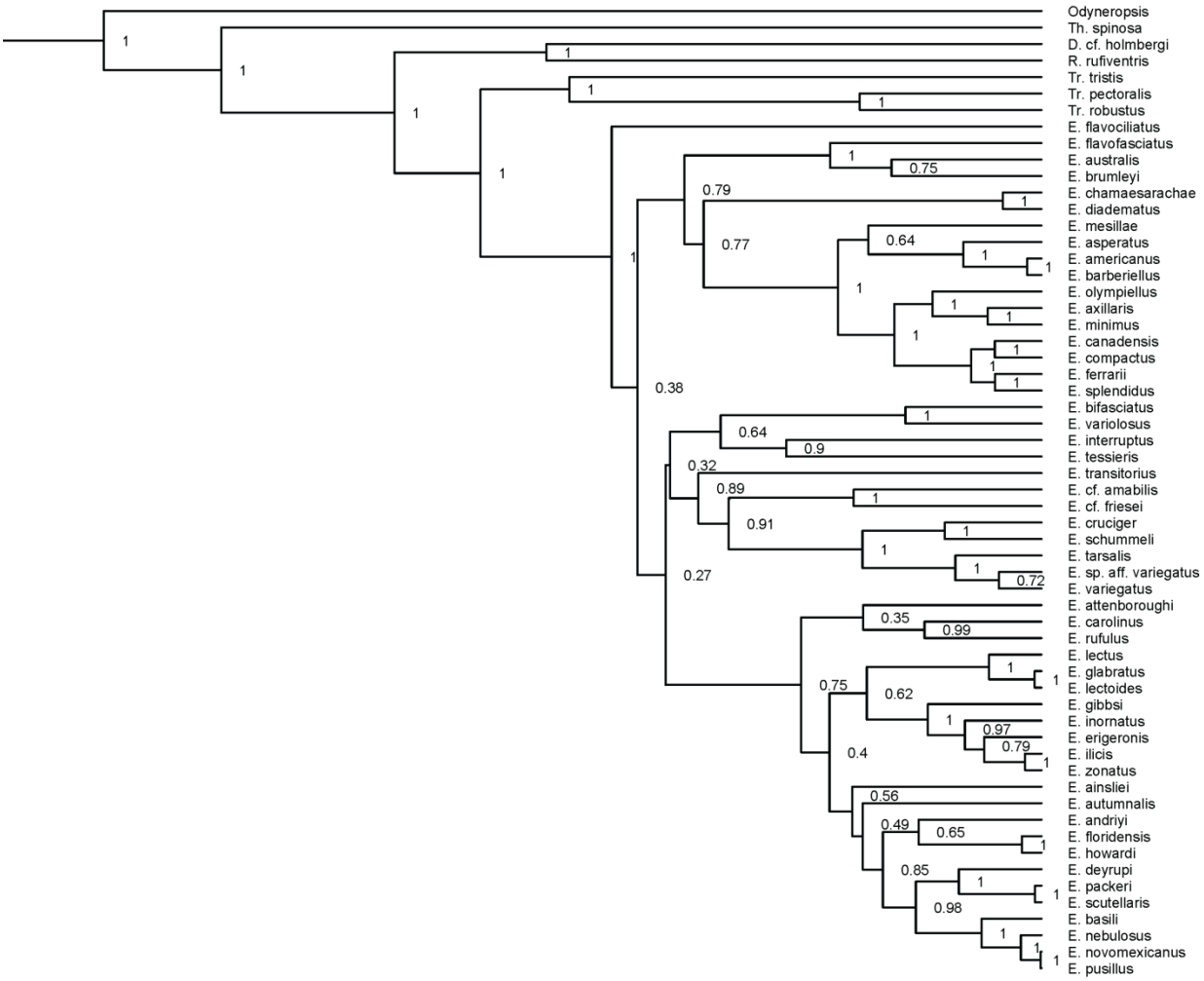


**Figure 1.** Dated phylogeny of *Epeolus* (based on the combined dataset of molecular sequences and morphological characters) obtained through phylogenetic analysis in BEAST 2 with a relaxed molecular clock model (maximum clade credibility tree is shown). Posterior probabilities are shown to the right of each node.

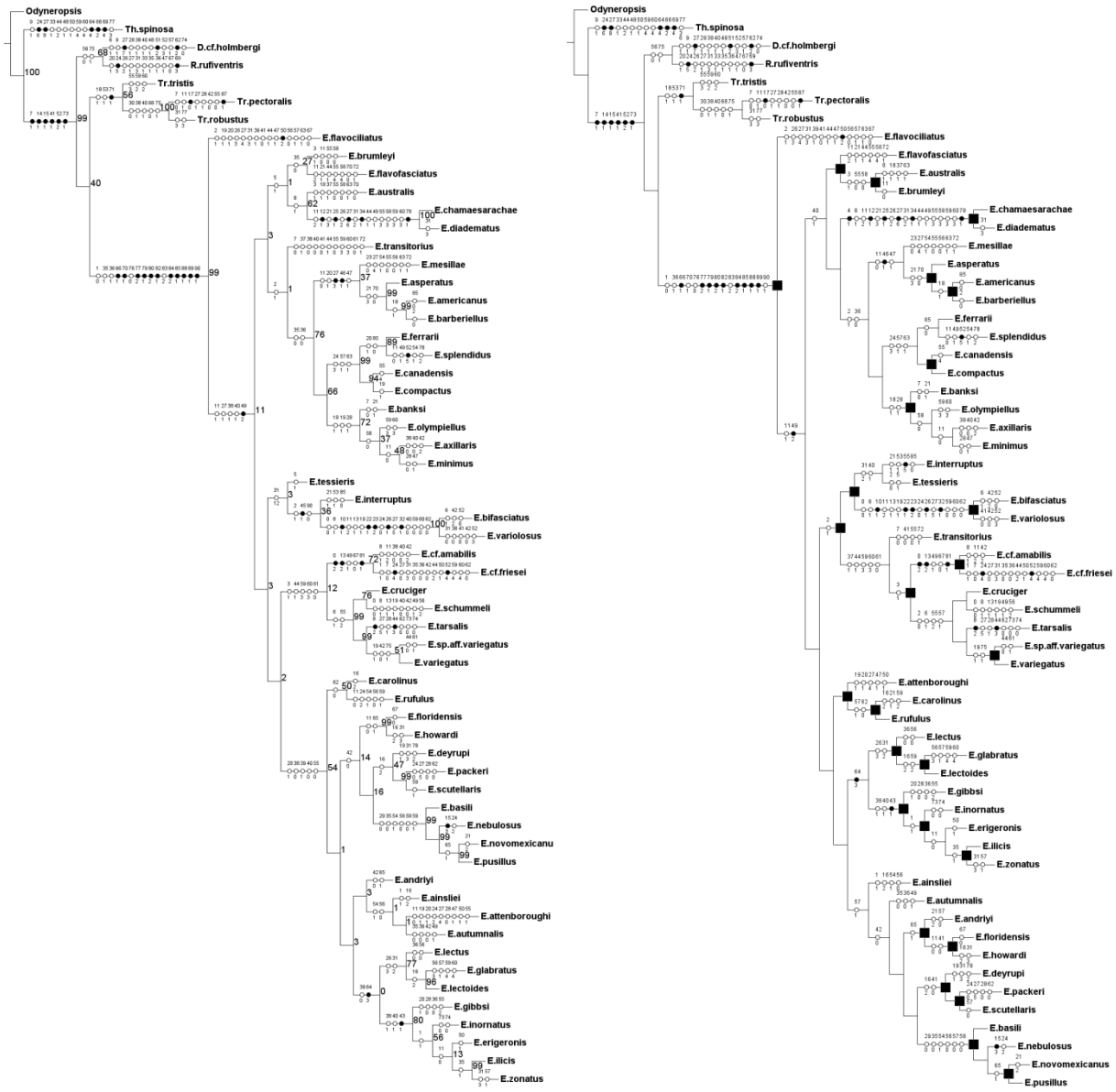


**Figure 2.** A comparison of phylogenies obtained through MP (left) and BI (right) analyses. Morphological characters are mapped onto both trees, with black circles indicating unique synapomorphic character states and empty circles indicating synapomorphic character states that appear elsewhere in the tree. Numbers above the circles are character identifiers (see Appendix for corresponding descriptions) whereas numbers below the circles are the assigned character states. GC values are shown to the right of each node in the MP tree. The tree on the right is topologically identical to the preferred (dated) tree from BEAST (Fig. 1), and was used in spatial analysis of vicariance. Black squares indicate nodes with distributional disjunctions.

*Colletes* phylogeny

Analyses in MrBayes and BEAST 2 resulted in topologies that were identical and well-supported. *Colletes* was recovered as a monophyletic group, with the crown age estimated to be between 19 and 18 Ma (Fig. 3). The dated phylogeny from BEAST was subsequently used in cophylogenetic analyses.

Cophylogenetic analyses

ParaFit analysis rejected the null hypothesis that speciation of the host clade occurred independently of speciation of the cleptoparasite clade, and vice versa (ParaFitGlobal = 5982385, P = 0.0036). The contribution of each individual host-parasite link to the overall congruence between the two trees was assessed, and 9 out of 23 associations were found to be significant ($P < 0.05$) whereas 4 were barely non-significant ($0.05 < P < 0.1$) (Fig. 3). There are indeed examples of closely-related species of *Epeolus* parasitizing a single host species or closely-related host species, as well as instances of one species of *Epeolus* parasitizing closely related species of *Colletes*. Although evidence for overall co-speciation was found, a comparison of the topologies of the phylogenies of *Epeolus* and *Colletes* show many instances in which diversification in one clade does not correspond to diversification in the other compared to the few instances of non-independent speciation (Fig. 3).

Regardless of the cost scheme implemented, reconciliation analysis consistently identified co-speciation as the least common event among those that culminated in the associations between extant species of *Epeolus* and *Colletes* (Table 1). By contrast, parasite losses (cases in which new species of *Colletes* escaped parasitism by *Epeolus* following divergence) seem to have occurred more frequently than all other types of events combined. When time constraints were removed (i.e. only topological congruence was required as evidence for co-speciation), the number of losses decreased substantially, but co-speciation was still an uncommon event (6 instances of co-speciation compared to 3 duplications, 8 duplications and host switches, 6 losses, and 5 failures to diverge [total cost = 30]) under the default cost scheme, which favors co-speciation the most.

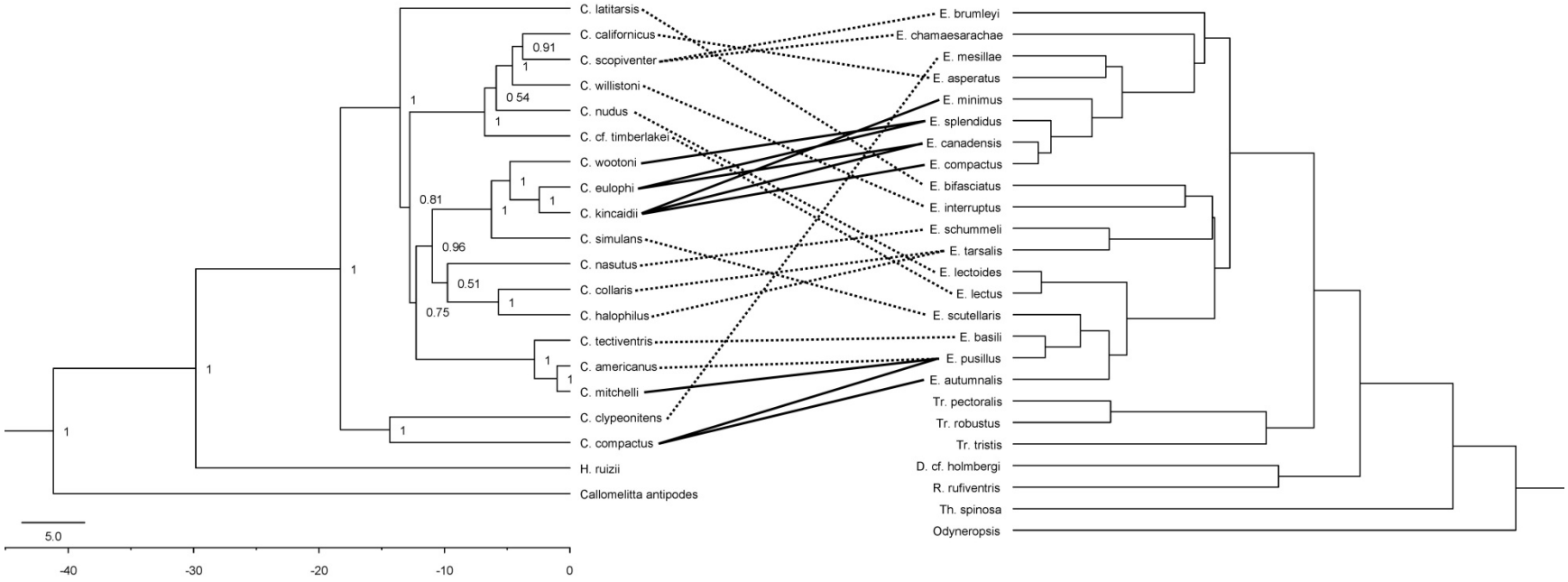


**Figure 3.** Dated phylogenies of *Colletes* (left) and *Epeolus* (right) generated in BEAST 2. Posterior probabilities are shown to the right of each node in the *Colletes* tree, and the scale represents time in millions of years. Associated host and cleptoparasite species are linked by a line. Solid lines indicate links that significantly contribute to phylogenetic non-independence of the two clades whereas dotted lines indicate non-significant links.

**Table 1.** Results of co-speciation analyses performed in Jane 4 indicating the number of inferred events of each type that best explain how relationships between extant species of *Epeolus* and *Colletes* formed given a particular cost structure. First on the list is the program's default cost scheme, with no cost assigned to co-speciation. Since a host switch first requires for a duplication event to occur (i.e. parasite speciation in the absence of host speciation), a host switch cannot be assigned a lower cost than duplication. By default, host switching is assigned twice the cost of any other event (except co-speciation) as it involves an extra step.

| Cost scheme | Number of co-speciation events | Number of duplication events | Number of duplication events & host switches | Number of losses (of *Epeolus*) | Number of failures (of *Epeolus*) to diverge | Total cost |
|---|---|---|---|---|---|---|
| 0, 1, 2, 1, 1 | 3 | 7 | 7 | 32 | 5 | 58 |
| 1, 1, 1, 1, 1 | 1 | 6 | 10 | 30 | 5 | 52 |
| 10, 1, 2, 1, 1 | 0 | 7 | 10 | 32 | 5 | 64 |
| 0, 10, 10, 1, 1 | 3 | 7 | 7 | 32 | 5 | 177 |
| 0, 1, 10, 1, 1 | 3 | 7 | 7 | 32 | 5 | 114 |
| 0, 1, 2, 10, 1 | 2 | 6 | 9 | 30 | 5 | 329 |
| 0, 1, 2, 1, 10 | 3 | 7 | 7 | 32 | 5 | 103 |

Biogeography

Dispersal Extinction Cladogenesis as implemented in the R package BioGeoBEARS indicates that the most probable range of the most recent common ancestors of both *Epeolus* and *Triepeolus* covered both the Eurasian and North American landmasses (Fig. 4). Within *Epeolus*, three clades (groups A, B, and D) show a high probability of having originated in the Nearctic, and one group (C) most likely has its origins in the Palaearctic. Within group D, there are six relatively recent clades (younger than 4 Ma) for which the most probable ancestral range included both Florida and the Nearctic. The analysis also suggests that Epeolini was originally a Neotropical clade.

Spatial analysis of vicariance in VIP identified 27 distributional disjunctions (i.e. instances of allopatric speciation), of which 13 are between species pairs and 14 are at internal

nodes (Fig. 2). Six disjunctions were found between species occurring in Eastern and Western North America (between *E. australis* and *E. brumleyi* [Onuferko 2018, Figs. 15 & 29], *E. canadensis* Mitchell and *E. compactus* Cresson [Onuferko 2018, Figs. 31 & 37], *E. carolinus* and *E. rufulus* [Onuferko 2018, Figs. 33 & 82], *E. chamaesarachae* and *E. diadematus* [Onuferko 2018, Figs. 35 & 42], *E. lectus* and the clade that includes *E. glabratus* and *E. lectoides* [Onuferko 2018, Figs. 54, 64, & 66], and *E. novomexicanus* and *E. pusillus* [Onuferko 2018, Figs. 74 & 80]), with the Great Plains forming the approximate barrier separating sister taxa. A barrier between peninsular Florida and other parts of Eastern North America was also inferred, separating five sister taxa (*E. floridensis* Mitchell and *E. howardi* Mitchell, *E. glabratus* and *E. lectoides*, *E. ilicis* and *E. zonatus*, *E. inornatus* and the clade that includes *E. erigeronis*, *E. ilicis*, and *E. zonatus*, and *E. packeri* and *E. scutellaris*). A boundary that roughly corresponds to the transition between the Rocky Mountains and the major hot deserts (Chihuahuan, Mojave, and Sonoran) immediately south of them separates *E. americanus* from *E. barberiellus* and *E. basili* Onuferko from the other members of the "*pusillus* group". A barrier was inferred separating each of two species (*E. andriyi* and *E. banksi*) present in an area encompassing Maryland and North Carolina from their sister clades that include species found in other parts of North America. Other distributional disjunctions were unique. *Epeolus asperatus* is confined to central and southern California whereas its sister clade [*E. americanus* + *E. barberiellus*] is represented elsewhere in North America. A disjunction was found between *E. gibbsi* (a species occurring in the Upper Midwest and southern Manitoba) and its sister clade, which includes four species occurring in the southern or southeastern United States. The area in which *E. flavofasciatus* occurs (between the Sierra Madre Occidental and Sierra Madre Oriental and where they join in the United States the Rocky Mountains) is largely disjoint from the range of its sister clade [*E. australis* + *E. brumleyi*]. The disjunction between *E. deyrupi* Onuferko and its sister clade [*E. packeri* + *E. scutellaris*] is questionable given that *E. deyrupi* and *E. packeri* are both endemic to peninsular Florida and southern Georgia. Similarly, *E. attenboroughi* Onuferko and *E. rufulus* both inhabit Colorado and New Mexico, but they are known from so few localities (Onuferko 2018, Figs. 13 & 82) that their areas of occupancy (based on the selected grid size and Moore neighborhood) show no overlap.

When the cost of distribution removal was set at the default, the total number of distributional disjunctions increased to 34, of which 12 are between species pairs and 22 are at

internal nodes. Disjunctions at deeper nodes and those separating Nearctic from Neotropical species and Old World species from one another should be interpreted with caution as they are based on limited taxon sampling (only for the Nearctic region were all known species included) and thus incomplete distributional data. However, there is a clear disjunction between the distributions of the species in the exclusively New World clade (group B) that includes *E. interruptus*, *E. tessieris*, and species in the "Trophocleptria group" and those comprising the exclusively Old World (i.e. African and Eurasian) clade (group C).

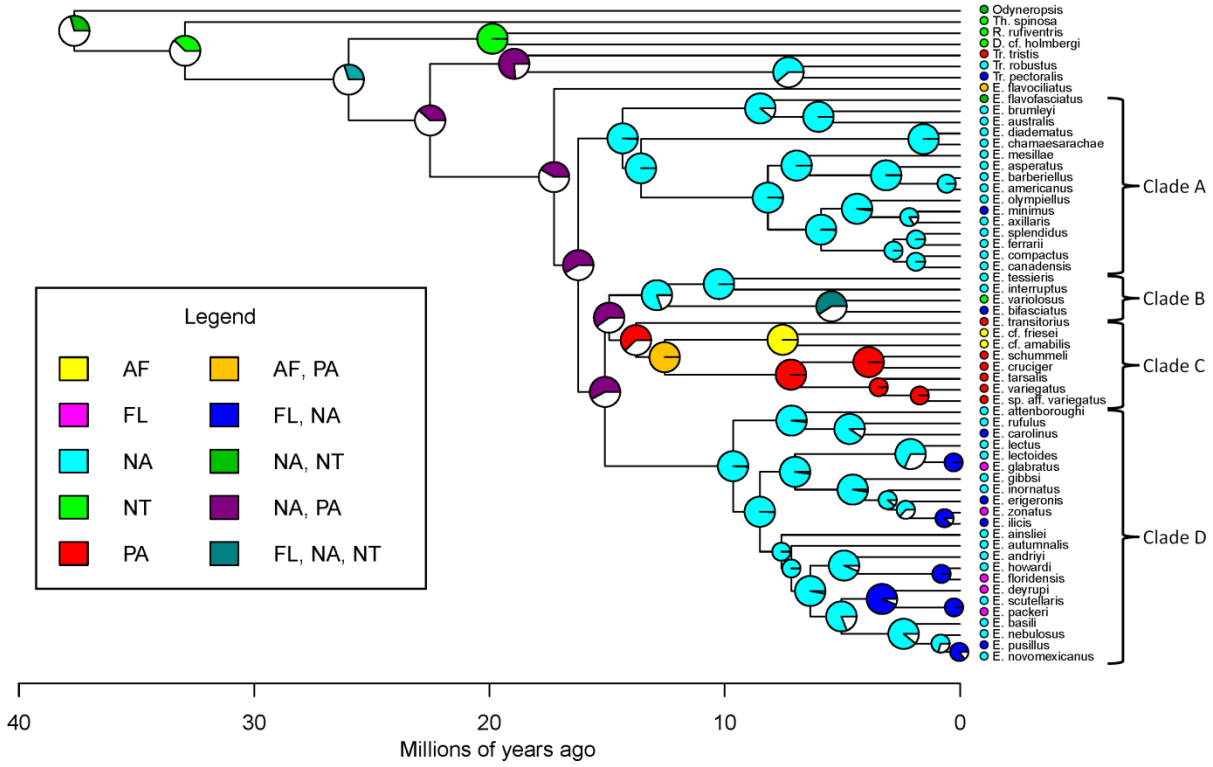


**Figure 4.** Reconstructed areas of occurrence for the most recent common ancestors of all taxa represented in the dated *Epeolus* phylogeny from BEAST (Fig. 1). The probability of an ancestral state is indicated as a pie chart. For simplicity, only one slice is shown at each node: that which corresponds to the most probable state; the white portion encompasses all other possible states. The five regions included in the analysis are as follows: the Afrotropic (AF), the Florida peninsula and coastal Georgia (FL), the Nearctic (including the Florida panhandle) (NA), the Neotropic (excluding the Florida peninsula) (NT), and the Palaearctic (PA). Circles immediately to the left of taxon names indicate known areas of occurrence.

**Discussion**

The present study strongly supports the monophyly of *Epeolus* and its breakdown into at least four major intrageneric groups. These results were consistent among the various methodologies employed. Despite this, it seems inadvisable at this time to propose subgenera for the genus. This is in part because the position of *E. flavociliatus* within *Epeolus* remains unclear, and because in the present study it was not possible to include representatives of all species that were at one time assigned to other genera that have since been synonymized under *Epeolus*. Yet, since each of the major groupings contains one or more species that have previously been assigned to multiple genera, one could simply affix the word "group" to an available name in reference to the more strongly supported clades. *Epeolus minimus* was once placed in *Argyroselenis*, so group A could be referred to as the "Argyroselenis group". The continued usage of "Trophocleptria group" as first suggested by Michener (2007) is sensible, and the term can be expanded to include *E. interruptus* and *E. tessieris* (also in group B). However, in light of the inferred topologies there is no justification for certain authorities (e.g. Moure et al. 2007) to continue to treat *Trophocleptria* as a separate genus. The exclusively Old World clade herein referred to as "group C" contains a species (*E. variegatus*) that was once placed in the now defunct genus *Monoepeolus*, but it is possible that the species previously placed in *Diepeolus* and *Oxybiastes* (*E. fallax* Morawitz and *E. bischoffi* (Mavromoustakis), respectively), which are now also considered to be synonyms of *Epeolus*, belong to this group as well. Unfortunately, due to a lack of material these species could not be included in the present study. Hence, until the classification of Old World *Epeolus* is better understood, group C could be called the "Monoepeolus group". *Epeolus glabratus* was at one point placed in its own genus, *Pyrrhomelecta*, so group D could be called the "Pyrrhomelecta group". The name seems appropriate as the clade includes a number of species conspicuously marked in red.

Among the outgroups are some interesting trends as well. Both BI and MP supported the monophyly of *Triepeolus* Robertson, with *T. tristis* (the only species occurring in Europe) appearing as sister to the Nearctic species included in the present study. This is consistent with the findings of Rightmyer (2004), whose morphological phylogeny placed the only two Palaearctic species (the other being *T. ventralis* (Meade-Waldo), not available for study) outside

of a monophyletic clade that included all of the New World *Triepeolus* included in that study. As in Cardinal et al. (2010), *Doeringiella* and *Rhinepeolus* Moure came out as sister to one another. Despite these consistencies, the topological position of some of the outgroups included in the present study is unexpected. The phylogenies of both Rightmyer (2004) and Cardinal et al. (2010) found Thalestriina to be a monophyletic group sister to Epeolina, whereas in the present study phylogenetic analysis rendered Thalestriina paraphyletic. The inclusion of additional thalestriine genera and species could resolve this inconsistency, as could the inclusion of *Rhogepeolus* Moure, which is morphologically intermediate between *Odyneropsis* and the rest of Epeolini (Rightmyer 2004). At present, however, no nuclear gene sequences are available for *Rhogepeolus*.

Co-speciation

This study is the first attempt to reconcile the phylogenies of any group of cleptoparasitic bees and their hosts. Tests of independence showed that species of *Epeolus* to some extent parasitize hosts that occupy corresponding positions in the phylogenetic tree. ParaFit analyses rejected the null hypothesis that speciation of one genus was independent (i.e. random) with respect to the other, indicating that there is at least some congruence between the *Epeolus* and *Colletes* phylogenies. Whereas co-speciation could not be ruled out, tests of independence and reconciliation analyses both suggest that it was an uncommon occurrence in the evolutionary history of the two genera. This is not surprising given that the number of convincing cases of co-speciation in the literature is rare (7% according to de Vienne et al. 2013), with host-shift speciation appearing to be far more prevalent. In the present study, when time constraints were imposed, the most commonly inferred event was parasite loss. One possible explanation for the prevalence of loss (a.k.a. sorting events) is that divergences might on multiple occasions have occurred within populations of a host species of *Colletes* that were not parasitized (i.e. outside the range of the associated *Epeolus*), such that when speciation occurred there were no cuckoos present, resulting in one of the new species of *Colletes* not being parasitized (i.e. the cleptoparasite ‘missed the boat’, Paterson and Gray 1997). To test this hypothesis, more information is needed about how *Colletes* diversified in the context of palaeoenvironmental conditions. At present, such an assessment is not feasible given the lack of a comprehensive

phylogeny for the genus (at least for North America, where the *Epeolus* fauna is well known) and that the taxonomy of Nearctic *Colletes* is problematic and needs to be revisited. In Stephen's (1954) revision, taxon concepts are incomplete for several species (e.g. there is no diagnosis for female *C. timberlakei* Stephen), and some have not yet been associated with conspecifics of the opposite sex (Onuferko 2018 gives one example of a species known only from males, *C. wickhami* Timberlake, that is most likely a junior synonym of a species known only from females, *C. scopiventer* Swenk).

Since most species of *Epeolus* have not yet been associated with their host species, and since most of those that have been were by means of circumstantial evidence, these results should be interpreted cautiously. Nonetheless, it seems unlikely that cleptoparasite-host co-speciation was primarily responsible for generating the great diversity of cuckoo bees present in the world today, especially in the context of the following considerations. First, many other cleptoparasitic bee genera (*Coelioxys* Latreille, *Nomada* Scopoli, *Sphecodes* Latreille, and *Triepeolus* Robertson to name a few of the larger ones [see Michener 2007, Alexander 1990, Michener 1978, and Rightmyer 2006, respectively, for overviews of host use]) are not restricted to a single host genus. Second, unlike obligate parasites that live on their hosts and have no dispersal stage (e.g. chewing lice [Phthiraptera: Trichodectidae] living on pocket gophers, Reed and Hafner 1997), cleptoparasitic bees are not constrained by their hosts' movements, which should make it easier for them to seek out new opportunities (i.e. nests of different host species). Lastly, most cuckoo bees (including other Epeolini) are probably far less specialized morphologically to parasitizing the nests of a single host taxon than *Epeolus* is on *Colletes*. Of course there are other means by which a cleptoparasitic bee can be specialized on a host bee (e.g. by behavioral adaptation and/or odor mimicry, see Tengö and Bergström 1977), but even if specialization evolved by means of reciprocal selection between associated cleptoparasite and host taxa, coevolution is not an indicator of widespread co-speciation. In the natural world, divergence as a result of specialization appears to occur more frequently following host-shift speciation than co-speciation (de Vienne et al. 2013). For coevolution to lead to diversification there needs to be a link between the coevolving traits and reproductive isolation, but evidence linking reciprocal selection to increased diversification is weak at best; in general, tests of coevolutionary diversification have focused on explaining macroevolutionary patterns rather than the underlying processes that gave rise to them (Althoff et al. 2014). Co-speciation may

occur when a single barrier appears that prevents gene flow between the separated host populations as well as the populations of their parasites or symbionts (de Vienne et al. 2013). It is therefore possible that the few inferred co-speciation events in the evolutionary history of *Epeolus* and *Colletes* resulted from simultaneous speciation in allopatry.

## Biogeography of *Epeolus*

Rightmyer (2004), who proposed a morphological phylogeny for Epeolini, predicted that *Epeolus* and *Triepeolus* diversified primarily in the Holarctic, and that extant representatives of those genera occurring in the Neotropics represent lineages that dispersed southwards from North America. This could explain the comparative paucity of species of both *Epeolus* and *Triepeolus* in South America, even though their host taxa (*Colletes* and various Eucerini, respectively) are highly diverse there (Rightmyer 2004). The results of the present study support such a prediction, with the Nearctic and Palaearctic regions identified as the most probable areas of occurrence for the most recent common ancestors of both genera. That the rest of the genera in Epeolini are restricted to South America and southern North America suggests that dispersal occurred from the New World to the Old World (with possible additional exchanges), sometime during the Miocene (23–14 Mya) and possibly across the Bering Land Bridge (BLB). Biogeographic analyses led Praz and Packer (2014) to infer that within Eucerini, which contains the vast majority of hosts of *Triepeolus* (Rightmyer 2006), there were interchanges between the New World, from which they originated, and the Old World (likely via the BLB) around the same time (23–13.9 Mya). Like Epeolini, *Colletes* is believed to have originated in South America (based on its diversity there and because the only closely related genus, *Mourecotelles* Toro & Cabezas *sensu lato*, is endemic to the continent, Michener 2007), from where it would have also dispersed first to North America and then the Old World (Kuhlmann et al. 2009). Based on their inferred crown ages, the BLB was the most likely route through which faunal exchanges in these lineages occurred between the Eastern and Western Hemispheres, until a global warm peak was reached c. 15 Mya (White et al. 1997). Conditions would have been less favorable for faunal exchanges more recently than 15 Mya as the area comprising the corridor experienced significant decreases in both summer and winter temperatures since (Wolfe 1994), and by about 5.3 Mya the Bering Strait opened (Gladenkov et al. 2002).

Inferences of dispersal/vicariance events focused on Nearctic *Epeolus* since all extant species known to occur in Canada and the United States were included in the present study. In North America, two barriers stand out as having played a recurring role in *Epeolus* speciation. A plurality of the inferred disjunctions between North American sister taxa is linked to an East–West divide. The appearance of mixed grass prairie (probably about 25 Mya, Coupland 1958), which transitions to shortgrass prairie and desert/semi-desert in western and southwestern North America, resulted in a climatic barrier. The Rocky Mountains are an additional physical barrier that bees would have had to get around or over to explain their current distributions. That the crown age of *Epeolus* is estimated to be between 18 and 17 million years old suggests that allopatric speciation was the result of dispersal over existing barriers rather than vicariance, since the Laramide orogeny that gave rise to the Rocky Mountains took place from 80 to 55 Mya (English and Johnston 2004) and the climate in the Great Plains and southwestern deserts was similar at the time *Epeolus* originated to what it is in those areas today.

In North America, the area between the Florida panhandle and peninsula also seems to have played a recurring role in *Epeolus* speciation. Spatial analysis of vicariance inferred disjunct distributions in five pairs of sister taxa that are geographically divided into species occurring in peninsular Florida/coastal Georgia versus those occurring elsewhere in Eastern North America. Most of these divergences appear to have been relatively recent (Fig. 4), and may be related to a single barrier: the Suwannee Straits, a strong unidirectional current that flowed from the Gulf of Mexico to the Atlantic Ocean through the Okefenokee Trough, which as recently as 1.75 Mya separated the Florida peninsula from the mainland (Bert 1986). During the early interglacial periods of the Pleistocene, the peninsula was reduced to a group of islands in central Florida (the Ocala highlands), which could have served as a refugium where the peninsular forms differentiated from the mainland forms (Neill 1957, Ellsworth et al. 1994). Even after the reduction in sea level and eventual bridging of the Straights, the Suwannee River, which now occupies much of the channel bed, continues to be a barrier for multiple species of local flying insects, which are not known to cross it (Neill 1957). A map showing the hypothesized barrier is given in Portnoy and Gold (2012), and the ranges of near Florida endemics *E. deyrupi*, *E. erigeronis*, *E. floridensis*, *E. glabratus*, *E. packeri*, and *E. zonatus* (Onuferko 2018, Figs. 40, 44, 50, 54, 78, & 90) fall almost entirely south of it. Four of these species exhibit unusually extensive red coloration, a widespread phenomenon among Florida

Hymenoptera (Deyrup and Eisner 2003). It is possible that the red-marked species form a mimetic complex (Deyrup and Eisner 2003), and that red coloration and reduced pubescence are traits that evolved recently and shortly after the peninsular forms diverged from the mainland forms.

These examples represent a subset of the instances of allopatric speciation events that were inferred through VIP. The list of Neotropical and Old World species is incomplete, so at this time it is not possible to explore the biogeography of species from those areas in greater detail. Moreover, the taxonomy of African, Asian, and Neotropical *Epeolus* is problematic, so for a truly global comprehensive biogeographic analysis based on actual distributional data these groups would first need to be revised. Although the overall extent to which dispersal/vicariance contributed to speciation in *Epeolus* remains unknown, it is likely that with greater taxon sampling the number inferred instances of allopatric speciation in the evolutionary history of the genus will increase.

## Conclusions

Current evidence suggests that *Epeolus* originated somewhere in the Holarctic region at a time when the Eurasian and North American landmasses were connected by the Bering Land Bridge. From there, the genus would have dispersed to the African and South American continents and into the southern hemisphere, where its present-day diversity (16 described spp. [11 in southern Africa and 5 in South America]) is much lower than in the Northern Hemisphere (94 described spp. [52 in Central and North America and 42 in Eurasia and northern Africa]) (Ascher and Pickering 2018, Bogusch 2018, Bogusch and Hadrava 2018, Moure et al. 2007, Onuferko 2018). Whereas the results of the present study suggest that diversification of *Epeolus* was to some degree influenced by its relationship with its host bee genus *Colletes*, it appears that co-speciation was an uncommon event in the evolutionary histories of both genera.

Most (24/36) speciation events that directly produced one or more extant species of *Epeolus* could be linked to some sort of barrier that presumably interrupted gene flow at the time of divergence. Whether or not the same barriers led to allopatric speciation in *Colletes* remains to be seen, but preliminary evidence suggests that in *Epeolus* (or at least Nearctic *Epeolus*) physical

barriers to gene flow were more important drivers of diversification than coevolution (i.e. reciprocal selection) between interacting cleptoparasite and host lineages.

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**Appendix I: Annotated list of morphological characters, which apply to both sexes unless stated otherwise**

0. Head width to length ratio (rounded to one decimal place): 0 ≤1.2 (Onuferko 2018, Fig. 91A); 1 1.3–1.4 (Onuferko 2018, Fig. 91B–D); 2 ≥1.5 (Fig. S2A). Note that *Thalestria spinosa* is sexually dimorphic with regard to this character, with females exhibiting state 1 and males exhibiting state 0, so it was coded as polymorphic.

1. Mandible: 0 with preapical tooth or angle (Onuferko 2017, Fig. 10B & C; Onuferko 2018, Fig. 3B, C, D, & F); 1 simple (Onuferko 2017, Fig. 10A; Onuferko 2018, Fig. 3A & E).

2. Preapical tooth (if present; otherwise "?"): 0 obtuse (Onuferko 2017, Fig. 10C; Onuferko 2018, Fig. 3B–D); 1 acute or forming right-angled triangle (Onuferko 2017, Fig. 10B; Onuferko 2018, Fig. 3F).

3. Labrum with two or more small denticles near or on apical margin: 0 present (Rightmyer 2004, Figs. 34, 35, & 37); 1 absent (Fig. S3A & B).

4. If present (otherwise "?"), number of paired denticles near or on apical margin of labrum: 0 two (Rightmyer 2004, Figs. 34, 35, & 37); 1 four (Fig S3C).

5. Labrum with two small submedian denticles (separated from apical margin by 1/4 to 2/5 the length of labrum): 0 absent; 1 present (Fig. S3B). Note that in some species (*Epeolus chamaesarachae*, *E. diadematus*, and *E. flavofasciatus*) there are apical/subapical as well as submedial denticles, so the two types are clearly not homologous.

6. Labrum with a distinct apicomedial tooth: 0 absent (Rightmyer 2004, Figs. 34 & 35); 1 present (Rightmyer 2004, Fig. 37). Note that in *E. variegatus* the apicomedial tooth is in a shallow concavity.

7. Clypeus medially with longitudinal impunctate line, which may be flat or faintly carinate, extending from supraclypeal area: 0 present (Fig. S4); 1 absent (Fig. S2B).

8. Frontal keel: 0 somewhat strongly raised (Onuferko 2018, Fig. 103B); 1 very strongly raised (Onuferko 2018, Fig. 103A); 2 not strongly raised but difficult to assess because supraclypeal area unusually expanded outward more or less evenly with the keel and laterally over part of the antennal socket (Rightmyer 2004, Fig. 169).

9. Frontal area with distinct depression above each antennal socket, to house the scape: 0 absent (Rightmyer 2004, Fig. 169); 1 present (Rightmyer 2004, Fig. 167).

10. Frontal area: 0 without a pair of granulose protrusions near upper mesal margins of compound eyes (Onuferko 2017, Fig. 6B; Onuferko 2018, Fig. 91B–D); 1 with a pair of granulose protrusions, each located near upper mesal margin of compound eye (Onuferko 2017, Fig. 6A; Onuferko 2018, Fig. 91A).

11. Upper gena/vertexal area with pair of protrusions: 0 absent/inconspicuous (Onuferko 2018, Fig. 91D); 1 present but not pronounced (Onuferko 2018, Fig. 91B); 2 present and pronounced (Onuferko 2018, Fig. 91A & C).

12. Vertexal area with pair of shiny, sparsely punctate or impunctate protrusions (located between second pair of protrusions [see character 11] so the two types are clearly not homologous): 0 absent (Onuferko 2017, Fig. 6A & B; Onuferko 2018, Fig. 91A, B, & D); 1 present (Onuferko 2018, Fig. 91C).

13. Vertexal area: 0 weakly convex (Onuferko 2017, Fig. 6B; Onuferko 2018, Fig. 91B–D); 1 strongly convex (Onuferko 2017, Fig. 6A; Onuferko 2018, Fig. 91A); 2 concave between compound eye and lateral ocellus (Fig. S2A).

14. Inner orbits of compound eyes of female: 0 parallel (Rightmyer 2004, Fig. 166); 1 converging below (Rightmyer 2004, Fig. 169).

15. Distance between lateral ocelli (rounded to nearest whole number): 0 1 MOD (Fig. S5A); 1 2 MOD (Fig. S5B); 2 3 MOD (Fig. S5C). Note that the largest observed value for state 0 is 1.40 MOD and the smallest observed value for state 1 is 1.65 MOD.

16. Preoccipital ridge: 0 absent (Fig. S6); 1 not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal (Onuferko 2017, Fig. 11B; Onuferko 2018, Fig. 95B); 2 joining hypostomal carina (approximately at 2/5 the length of the proboscidial fossa) (Onuferko 2017, Fig. 11A; Onuferko 2018, Fig. 95A) or almost joining hypostomal carina, from which it is separated by less than 1 MOD at its terminal. Note that the preoccipital ridge joins the hypostomal carina only in *E. ainsliei,* so for the character to be informative for this species "joining" and "almost joining" were combined into one state.

17. Preoccipital ridge (if present; otherwise "?"): 0 limited to gena (Rightmyer 2004, Fig. 33); 1 discontinuous, on gena and dorsal margin behind vertexal area (Rightmyer 2004, Fig. 32); 2 continuous from gena to dorsal margin behind vertexal area, forming a rounded curve (Rightmyer 2004, Fig. 30).

18. Maxillary palpus: 0 two-segmented (Rightmyer 2004, Figs. 27 & 28); 1 three-segmented (Rightmyer 2004, Fig. 26).

19. Scape (excluding radicle) with greatest length (rounded to one decimal place): 0 ≥1.8 × greatest width (Fig. S7A); 1 ≤1.7 × greatest width (Fig. S7B). Note that for consistency the width of the scape of *Doeringiella* was measured at the apex (as in all the other species), not the basal swelling where it is slightly wider.

20. F2 of female (L/W ratio rounded to one decimal place): 0 noticeably longer than wide (L/W ratio = 1.2–1.7) (Onuferko 2017, Fig. 14B; Onuferko 2018, Fig. 96B, D, & F); 1 about as long as wide (0.9 ≤ L/W ratio ≤ 1.1) (Onuferko 2017, Fig. 14A; Onuferko 2018, Fig. 96A, C, & E).

21. F2 of male (L/W ratio rounded to one decimal place): 0 much longer than wide (L/W ratio ≥1.5) (Fig. S8A); 1 somewhat longer than wide (L/W ratio = 1.2–1.4) (Fig. S8B); 2 about as long as wide (0.9 ≤ L/W ratio ≤ 1.1) (Fig. S8C); 3 wider than long (L/W ratio = 0.8) (Fig. S8D). Note that the F2 of the male is nearly always shorter than the F2 of the female, but its length (relative to the width of the F2) cannot consistently be inferred from the length of the F2 of the female, so both sexes were scored separately for this character.

22. Pronotal collar, anterior margin (dorsal view): 0 convex (Fig. S9C); 1 straight or nearly so (Fig. S9B).

23. Pronotal collar, medial length (dorsal view): 0 ~1/3 MOD or less (Fig. S9A); 1 2/5 to 4/5 MOD (Fig. S5B); 2 ~1 MOD or more (Fig. S9B). Note that although scored as 0 the pronotal collar is not visible in *Doeringiella* cf. *holmbergi* medially as the mesoscutum overhangs the pronotum at the midline (Rightmyer 2004, Fig. 43).

24. Mesoscutum: 0 sparsely covered in appressed pale tomentum or with pale tomentum limited to margins or absent (Onuferko 2018, Figs. 26B, 77B, & 89B); 1 with paramedian bands of appressed pale tomentum, which may be weak (e.g. Onuferko 2018, Fig. 16B) or pronounced (e.g. Onuferko 2018, Fig. 73B); 2 densely covered in appressed pale tomentum, at least anteromedially (Onuferko 2018, Figs. 12B, 71B, & 81B); 3 with anteromedial patch of appressed pale tomentum, usually chevron-, horseshoe-, or V-shaped and narrowed anterolaterally (Figs. 30B, 36B, 38, 45B) but sometimes semicircular (Fig. 85B); 4 with mixed pale and dark hairs sparse and erect, not appressed (Fig. S10A); 5 with longitudinal band of appressed setae on midline (Fig. S9C); 6 densely covered in minute, appressed, plumose, scale-like, metallic blue or green tomentum (Fig. S9D).

25. Mesoscutum with paramedian bands: 0 simple (Onuferko 2018, Figs. 4B, 8B, 10B, 14B, 16B, 18B, 24B, 28B, 32B, 39B, 43B, 47B, 49B, 51B, 55B, 57B, 59B, 61B, 63B, 65B, 67B, 69B, 73B, 75B, 79B, 83B, & 87B); 1 encircling black spots on anterior margin (Onuferko 2018, Figs. 34B & 41B).

26. Mesoscutum, mesoscutellum, and axilla: 0 with punctures dense (i≤1d) and somewhat coarse (≈ 2–3 metasomal tergal puncture diameters) (Onuferko 2018, Figs. 4D, 6D, 8D, 10D, 14D, 16D, 18D, 20D, 22D, 24D, 28D, 30D, 32D, 36D, 39D, 43D, 45D, 47D, 49D, 51D, 55D, 57D, 59D, 61D, 69D, 71D, 73D, 75D, 77D, 79D. 81D, 83D, 85D, 87D & 89D); 1 with punctures dense (i≤1d) and very coarse (most > 3 metasomal tergal puncture diameters) (Onuferko 2018, Fig. 26D); 2 with punctures dense anteriorly (i≤1d), sparser posteriorly (most i>1d), and somewhat coarse (≈ 2–3 metasomal tergal puncture diameters) (Onuferko 2018, Figs. 34D & 41D); 3 with punctures sparse (most i>1d) and very coarse (most > 3 metasomal tergal puncture diameters) (Onuferko 2018, Figs. 53D, 63D, & 65D).

27. Mesopleuron of female: 0 with hairs sparse and erect, not appressed (Fig. S10B); 1 with two sparsely hairy or hairless patches (one behind pronotal lobe beneath base of fore wing (hypoepimeral area), a larger circular patch occupying much of ventrolateral half of mesopleuron) (Onuferko 2018, Fig. 92A & 92C); 2 with upper half densely hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare (Fig. S11D); 3 with upper half hairy throughout, ventrolateral half nearly bare (Onuferko 2018, Fig. 6A & C, 10A & C, & 22A & C); 4 almost entirely obscured by white tomentum (hypoepimeral area and ventrolaterally somewhat more sparsely hairy) (Onuferko 2018, Figs. 12A & C & 67A & C); 5 mostly bare or sparsely hairy, except along margins (Onuferko 2017, Fig. 4A; Onuferko 2018, Fig. 92D); 6 with upper half densely hairy, although scrobe visible; ventrolateral half nearly bare (Onuferko 2018, Figs. 92I & J); 7 with hairs long and dense anteriorly and ventrally along margins and around hypoepimeral area, otherwise covered in dense but very short appressed hairs (Fig. S11A); 8 with small spot of white tomentum below scrobe, otherwise evenly covered in metallic blue-green tomentum (Fig. S11C).

28. Mesopleuron of male: 0 with hairs not denser compared to that of female (Onuferko 2018, Figs. 12A & C & 87A & C); 1 with hairs at least somewhat denser compared to that of female (Onuferko 2018, Figs. 4C, 16C, 24C, 32C, 49C, 55C, 57C, 65C, 71C, 73C, 79C, 81C, & 89C).

29. Mesopleuron of male (if different than that of female; otherwise “?”): 0 excluding hypoepimeral area, entirely obscured by white tomentum (Onuferko 2018, Figs. 24C, 71C, 73C,

& 79C); 1 similar to state 1 of character 27 (with two sparsely hairy or hairless patches), but with tomentum at least somewhat denser compared to that of female (Onuferko 2018, Figs. 4C, 16C, 32C, 49C, 55C, 57C, 65C, 81C, & 89C); 2 similar to state 1 of character 27 (with hairs long and dense anteriorly and ventrally along margins and around hypoepimeral area, otherwise covered in dense but very short appressed hairs), but with tomentum denser compared to that of female (Fig. S11B).

30. Mesopleuron with long, erect simple setae among shorter branched hairs: 0 present (Rightmyer 2008, Fig. 166); 1 absent (Onuferko 2017, Fig. 15).

31. Mesopleuron: 0 densely (i≤1d) and more or less evenly punctate (Onuferko 2017, Fig. 4C; Onuferko 2018, Fig. 92B, D, E, F, G, K, & L); 1 with larger and denser (i≤1d) punctures in upper half than ventrolateral half (i>1d) (Onuferko 2017, Fig. 4A); 2 with denser (i≤1d) punctures in upper half than ventrolateral half (i>1d), but punctures similar in size throughout mesopleuron (Onuferko 2017, Fig. 4B & D; Onuferko 2018, Fig. 92A, H, & I); 3 with punctures in ventrolateral half somewhat sparser (i≤2d) than in upper half (i≤1d) (Onuferko 2018, Fig. 92C & J). Note that *Triepeolus pectoralis* females exhibit state 2 whereas males exhibit state 0 so the species was treated as polymorphic with respect to this character.

32. Mesoscutellum with a distinct ridge overhanging its posterior surface: 0 absent (Onuferko 2017, Fig. 17A & B; Onuferko 2018, Figs. 94A & B & 102A & B); 1 present (Fig. S12).

33. Mesoscutellum with a pair of prominent mammiform tubercles: 0 absent, although mesoscutellum usually bigibbous to some degree (Onuferko 2017, Figs. 5, 8, & 13); 1 present, distinctly pointed (Fig. S9C & D).

34. Mesoscutellum medially with a distinct longitudinal strip of appressed pale tomentum: 0 absent (Onuferko 2017, Fig. 5, 8, & 13); 1 present (Figs. 34D, 41D, & 67D).

35. Mesoscutellum (color): 0 black (Onuferko 2018, Fig. 6B & D); 1 ferruginous to some degree, at least in conspecifics (Onuferko 2018, Fig. 4B & D).

36. Axilla (color): 0 black except sometimes tip ferruginous (Onuferko 2018, Fig. 18B & D); 1 ferruginous beyond tip, at least in conspecifics (Onuferko 2018, Figs. 8B & D & 24B & D).

37. Axilla and mesoscutellum with color sexual dimorphism: 0 absent (Onuferko 2018, Figs. 69D & 101A); 1 present (in female ferruginous; in male black or nearly so) (Bogusch and Hadrava 2018, Figs. 23, 24, 79, 80, 108, & 109).

38. Axilla: 0 large, its lateral margin at least half as long as mesoscutellar width (Onuferko 2017, Fig. 13A & B); 1 small, its lateral margin less than half as long as mesoscutellar width (Onuferko 2017, Fig. 13C & D).

39. Axilla with lateral margin: 0 relatively straight or somewhat concave (Onuferko 2018, Figs. 6D, 10D, 14D, 18D, 20D, 22D, 26D, 28D, 30D, 34D, 36D, 45D, 47D, 51D, 53D, 57D, 59D. 61D, 65D, 67D, 69D, 75D, 85D, 87D, & 89D); 1 arcuately convex (Onuferko 2018, Figs. 4D, 8D, 12D, 16D, 24D, 32D, 39D, 43D, 49D, 55D, 63D, 71D, 73D, 77D, 79D, 81D, & 83D). Note that although in *Epeolus variolosus* the lateral margin of the axilla is unusually denticulate (Fig. S9B), it is approximately straight and clearly not arcuately convex, so the species was scored as exhibiting state 0.

40. Axilla with tip: 0 extending to or beyond 2/3 the length of mesoscutellum (Onuferko 2018, Figs. 4D, 8D, 12D, 16D, 18D, 24D, 26D, 32D, 39D, 49D, 53D, 55D, 63D, 71D, 73D, 77D, 79D, 81D, & 83D); 1 extending to less than 2/3 the length of mesoscutellum (Onuferko 2018, Figs. 6D, 10D, 14D, 20D, 22D, 28D, 30D, 34D, 36D, 41D, 43D, 45D, 47D, 51D, 57D, 59D, 61D, 65D, 67D, 69D, 75D, 85D, 87D, & 89D).

41. Axilla with tip (if extending to no less than 2/3 the length of mesoscutellum): 0 extending as far back as or beyond posterior margin of mesoscutellum (Onuferko 2018, Figs. 39D, 49D, 55D, 77D, & 83D); 1 not extending as far back as posterior margin of mesoscutellum (Onuferko 2018, Figs. 4D, 8D, 12D, 16D, 18D, 24D, 26D, 32D, 53D, 63D, 71D, 73D, 79D, & 81D).

42. Axilla with free portion: 0 less than 2/5 but more than 1/4 its entire medial length (Onuferko 2018, Figs. 8D, 14D, 16D, 20D, 24D, 28D, 34D, 41D, 47D, 49D, 55D, 69D, 71D, 73D, 75D, 77D, 79D, & 83D); 1 at most 1/4 its medial length (Onuferko 2018, Figs. 6D, 10D, 22D, 30D, 45D, 61D, 67D, 85D, & 87D); 2 ~2/5 its entire medial length or longer (Onuferko 2018, Figs. 4D, 12D, 18D, 32D, 43D, 51D, 53D, 57D, 59D, 63D, 81D, & 89D).

43. Axilla with free portion (if ~2/5 its entire medial length or longer; otherwise "?"): 0 angled posteriorly (Onuferko 2018, Figs. 4D, 12D, 18D, 32D, 53D, 63D, & 81D); 1 angled laterally (Onuferko 2018, Figs. 43D, 51D, 57D, 59D, & 89D).

44. Metanotum with tomentum: 0 appressed, uniformly pale yellow/off white (Onuferko 2018, Fig. 94); 1 appressed, pale yellow/off white laterally, darker (gray, brown, or black) medially (Onuferko 2017, Fig. 17); 2 erect, dark gray or black (Fig. S10B); 3 sexually dimorphic: in female appressed, uniformly black; in male appressed, pale yellow/off white laterally, darker (gray, brown, or black) medially.

45. Metanotum with blunt median process: 0 absent; 1 present. Note that in *Epeolus bifasciatus* and *E. variolosus* the metanotum varies in the degree to which it is medially convex and in some specimens there is no distinct process. However, given the presence of a distinct process in other species in the "Trophocleptria group" both were scored as exhibiting state 1.

46. Fore wing: 0 with three submarginal cells (the second submarginal crossvein is rarely incomplete) (Onuferko 2018, Fig. 4A); 1 commonly or consistently with two submarginal cells (Onuferko 2018, Figs. 6A & B, 22C, & 67A & C). Note that only in *E. mesillae* the fore wing consistently has two submarginal cells, whereas in the three other species scored as exhibiting state 1 the fore wing sometimes has three submarginal cells, so for the character to be informative the latter could not be coded as polymorphic.

47. Fore wing, radial cell with setae: 0 abundant in costal half, virtually absent along M+Cu (Fig. S13B); 1 very sparse, scattered, generally along margins of Sc+R and M in posterior half (Fig. S13A).

48. Mesofemur of male ventrally with long setae: 0 absent (Fig. S14B); 1 present (Fig. S14A).

49. Mesotibia dorsally with thick, spine-like setae (these may be conspicuously darker and longer than surrounding pale hairs): 0 absent (Fig. S15A); 1 numerous (Fig. S15B); 2 few, scattered (Fig. S15C).

50. Metatibia anteriorly and dorsally with protuberant bases of spine-like setae: 0 present, enlarged (Rightmyer 2004; Fig. 174); 1 present, not enlarged (Fig. S16A); 2 absent (Fig. S16B).

51. Basitibial plate: 0 absent (or perhaps present but if it is then it cannot be distinguished from the rest of the tibia since it is not outlined by a carina) (Fig. S17C); 1; partially outlined by carina (Fig. S17B); 2 fully outlined by carina (Fig. S17A).

52. T1 with pale tomentum: 0 present basally and forming fascia, absent apically and laterally (Fig. S18A); 1 present only as a pair of small basolateral patches; 2 present, forming bands on all sides (i.e. T1 with basal fascia, apical fascia, and longitudinal bands uniting them on each side); 3 present apically and forming fascia, reduced or absent basally and laterally; 4 absent, tergum entirely without appressed pale hairs (Fig. S18B); 5 present basally (as silvery white fascia) and apically (as bright yellow fascia), with little space in between (i.e. without longitudinal bands). Note that *Epeolus tarsalis* is sexually dimorphic with regard to this character, with females exhibiting state 3 (Fig. S18C) and males exhibiting state 2, so it was coded as polymorphic.

53. T1 basal fascia (if present; otherwise "?"): 0 narrowed or narrowly interrupted medially but not by a distinct patch of black tomentum (Onuferko 2017, Fig. 9C–F); 1 distinctly interrupted medially by a small patch of black tomentum (Rightmyer 2008, Fig. 188; Onuferko 2017, Fig. 9A).

54. T1 apical fascia (if present; otherwise "?"): 0 interrupted medially; 1 complete.

55. T1 with discal patch (if shape clearly defined by presence of bands of pale tomentum on all sides [i.e. character is applicable only to taxa that exhibit state 2 of character 52; otherwise “?”]): 0 quadrangular to elliptical and very wide, the basal and apical fasciae only narrowly joined laterally when viewed dorsally; 1 quadrangular and not so wide, the longitudinal band is at least half as wide as the breadth of the apical fascia when viewed dorsally; 2 variable, quadrangular to elliptical and occasionally very wide in conspecifics, the basal and apical fasciae only narrowly joined laterally when viewed dorsally; 3 diamond shaped or in the shape of a pointed oval; 4 triangular or semicircular with lateral sides straight or convex; 5 very wide, the basal and apical fasciae only narrowly joined laterally and forming rounded triangle with lateral sides concave.

56. T2 apical fascia (if present; otherwise “?”): 0 complete; 1 interrupted medially; 2 interrupted medially and laterally; 3 reduced to a pair of small posterolateral patches.

57. T2 apical fascia (if present; otherwise “?”): 0 with anterolateral extensions of pale tomentum (Onuferko 2018, Fig. 14A–C), which in some species may be faint or short and lacking in conspecifics (Onuferko 2018, Fig. 8A & B); 1 without anterolateral extensions (Onuferko 2018, Fig. 4A–C).

58. T2 fascia with anterolateral extensions of pale tomentum (when present): 0 distinct, lobe-like, not much sparser than that comprising apical fascia; 1 very short (i.e. not lobe-like); 2 much sparser than that comprising apical fascia; 3 paired, not much sparser than that comprising apical fascia; 4 variable, but occasionally distinct, lobe-like, not much sparser than that comprising apical fascia.

59. T3 apical fascia: 0 absent; 1 complete; 2 interrupted medially; 3 interrupted medially and laterally; 4 reduced to a pair of small posterolateral patches.

60. T4 apical fascia: 0 absent; 1 complete; 2 interrupted medially; 3 interrupted medially and laterally; 4 reduced to a pair of small posterolateral patches.

61. T1–T4 apical fasciae (if all interrupted medially; otherwise "?"): 0 very widely interrupted medially, especially on T1 and T2 (for 1/5 to 2/5 the width of the apical margin of the tergum (in dorsal view)) (Fig. S18C); 1 not so widely interrupted medially (for less than 1/5 the width of the apical margin of the tergum (in dorsal view)) (Onuferko 2018, Figs 10B, 18B, 20B, 32B, 34B, 39B, 41B, 49B, 55B, 61B, 63B, & 87B).

62. T5 of female: 0 without distinct patch(es) of pale tomentum surrounding pseudopygidial area, although few sparsely scattered pale hairs sometimes present (Onuferko 2018, Fig. 97A); 1 with one or two patches of pale tomentum preceding or anterolateral/lateral to pseudopygidial area (Onuferko 2018, Fig. 97B–G & I); 2 without distinct patch(es) of pale tomentum surrounding pseudopygidial area, but nearly entire tergum covered in very short, minute hairs that are only faintly lighter than the underlying integument (Fig. S19A).

63. T5 of female with pale tomentum: 0 present as two distinct widely separated patches anterolateral/lateral to pseudopygidial area (note that in *Thalestria spinosa* these are extremely short and present only along the lateral margins of the tergum) (Onuferko 2018, Fig. 97B, F, & G); 1 present as large continuous patch (Onuferko 2018, Fig. 97D, E, & I) (or two large narrowly separated patches, Onuferko 2018, Fig. 97C) bordering pseudopygidial area.

64. Pseudopygidial area of female: 0 with an incomplete mid-dorsal depression and medioapical slit on the apical margin (Rightmyer 2004, Figs. 180A & 181), apical half with patch of shiny setae; 1 without a mid-dorsal depression and apical slit, patch of setae ovate (i.e. round, more or less in the shape of a circle) (Onuferko 2017, Fig. 2C); 2 without a mid-dorsal depression and apical slit, patch of setae lunate (i.e. arched, more or less in the shape of a semicircle) (Onuferko 2018, Fig. 97A–E & I); 3 without a mid-dorsal depression and apical slit, patch of setae campanulate (i.e. in the shape of a bell) (Onuferko 2018, Fig. 97F–H); 4 without a mid-dorsal depression and apical slit, patch of setae not clearly delimited from rest of tergum, but apical transverse area densely covered with long, stiff hairs (Fig. S19B).

65. If pseudopygidial area of female lunate (otherwise “?”), its apex: 0 at least twice as wide as medial length (Onuferko 2018, Fig. 97A, C, D, & I); 1 less than twice as wide as medial length (Onuferko 2018, Fig. 97B & E).

66. Pseudopygidial area setae of female, primary color: 0 golden (Onuferko 2017, Fig. 2C); 1 silvery (Onuferko 2018, Fig. 97); 2 black or dark brown/gray (Fig. S19B).

67. Metasomal terga with punctures: 0 sparse (most i>1d) (Onuferko 2017, Fig. 12B; Onuferko 2018, Fig. 93B & C); 1 dense (most i≈1d) (Onuferko 2017, Fig. 12A; Onuferko 2018, Fig. 93A).

68. Pygidial plate of female medially with longitudinal groove: 0 present (Fig. S20A); 1 absent (Fig. S20B).

69. Pygidial plate of female (in posterior view) with apicoventral surface: 0 with a pair of lateral enlarged triangular processes, which appear to be derived from both the lateral and ventral surfaces of T6 (Fig. S21); 1 with a pair of lateral scroll-like processes, which appear to be derived from the lateral surface of T6 (Rightmyer 2004, Fig. 178); 2 with a pair of submedial flattened, rounded processes, which appear to be derived from the ventral surface of T6 (Rightmyer 2004, Fig. 176, these processes are sometimes very reduced); 3 with a pair of mediolateral triangular projections, which appear to be derived from the ventral surface of T6; 4 with a single rounded medial process, which appears to be derived from the ventral surface of T6 (Rightmyer 2004, Fig. 175).

70. Pygidial plate of male: 0 elongate and apically narrowed (Onuferko 2017, Fig. 1C & D); 1 broadly rounded or subtruncate (note that in *Epeolus deyrupi* the male pygidial plate is sometimes notched apically) (Onuferko 2017, Fig. 1A & B).

71. Pygidial plate of male with distal surface: 0 not distinctly differentiated from dorsal surface of plate (Onuferko 2017, Fig. 1B); 1 downturned, at an obtuse angle to dorsal surface of plate (Rightmyer 2004, Fig. 19).

72. S3 of male with setae at apex: 0 short, straight (Onuferko 2018, Fig. 100); 1 long, curved (Rightmyer 2008, Figs. 241 & 242). Note that in most Epeolini the S3 of the male does not have the long, curved setae usually present on S4 and S5.

73. S4 of male with setae at apex: 0 short, straight (Onuferko 2018, Fig. 100B); 1 long, curved (Onuferko 2018, Fig. 100A).

74. S5 of male with setae at apex: 0 short, straight (Onuferko 2018, Fig. 100B); 1 long, curved (Onuferko 2018, Fig. 100A). Note that the presence of long, curved setae on S4 does not always coincide with the presence of long, curved setae on S5 (as in *Doeringiella* cf. *holmbergi*), and vice versa (as in *Thalestria spinosa*), so the two sterna were scored separately.

75. S5 of female with apex: 0 more or less on same plane as disc (Onuferko 2018, Fig. 61A); curved posteroventrally (Rightmyer 2008, Fig. 36).

76. S6 of female with length of sclerotized area of disc: 0 equal to or greater than length of apical lateral processes (Rightmyer 2004, Figs. 12 & 13); 1 much less than length of apical lateral processes (Rightmyer 2004, Figs. 7, 9, & 10). Note that all *Epeolus* spp. were presumed to exhibit state 0, including the following that were not dissected because they are exceptionally rare in collections: *E. andriyi*, *E. banksi*, *E. gibbsi*, *E. nebulosus*, *E. rufulus*, and *E. tessieris*.

77. S6 of female with apical margin of disc: 0 concave; 1 concave medially, with a slight convexity laterally (Rightmyer 2004, Fig. 7); 2 lobelike, evenly convex or with a median emargination (Rightmyer 2004, Fig. 13); 3 straight, roughly perpendicular to the inner margins of the apical lateral processes (Rightmyer 2004, Figs. 9 & 10). Note that all *Epeolus* spp. were presumed to exhibit state 2, including the following that were not dissected because they are exceptionally rare in collections: *E. andriyi*, *E. banksi*, *E. gibbsi*, *E. nebulosus*, *E. rufulus*, and *E. tessieris*.

78. If convex (otherwise “?”), S6 of female with apical margin of disc: 0 without median emargination (Onuferko 2017, Fig. 2B); 1 bifid (with a pronounced median emargination) (Fig. S22B); 2 with a slight median emargination (Fig. S22C).

79. S6 of female, apical lateral processes: 0 subparallel and rodlike (Rightmyer 2004, Figs. 7, 9, 10, & 12); 1 convergent and spatulate (Rightmyer 2004, Fig. 13).

80. S6 of female with principal setae: 0 short, apically rounded or bluntly pointed (Rightmyer 2004, Fig. 12); 1 long, apically pointed and hooked (Rightmyer 2004, Figs. 7 & 10); 2 forming minute, pointed denticles (Rightmyer 2004, Fig. 13).

81. If present (otherwise “?”), number of minute, pointed denticles on each process of S6: 0 less than 15 (Onuferko 2017, Fig. 2A); 1 15 or more (Fig. S22A).

82. S6 of female with principal setae directed: 0 medioventrally to ventrally (Onuferko 2017, 2C & D); 1 laterally (Onuferko 2017, 2A & B).

83. S6 of female with marginal setae: 0 present along entire apical margin of disc (Rightmyer 2004, Figs. 12 & 13); 1 absent between apical lateral processes where disc is reduced to a narrow transverse bar (Rightmyer 2004, Figs. 7, 9, & 10).

84. S6 of female with tip of each apical lateral process: 0 flat, forming a small rounded plate (Rightmyer 2004, Figs. 11 & 12); 1 flat, forming a pointed (usually three-pronged) plate (Rightmyer 2004, Fig. 7); 2 not flat, more spoonlike than platelike (Rightmyer 2004, Fig. 13).

85. S7 of male apically with median emargination: 0 present (Rightmyer 2004, Fig. 16); 1 absent (Rightmyer 2004, Figs. 68–76).

86. S7 of male with lateral lobes of distal process: 0 not extending as far posteriorly as interlobal area (Rightmyer 2004, Fig. 81); 1 extending further posteriorly than interlobal area (Rightmyer 2004, Figs. 68–76).

87. S7 of male ventrally with setae in emargination formed near lateral lobe of distal process: 0 absent (Rightmyer 2004, Fig. 85); 1 present (Rightmyer 2004, Figs. 86–95).

88. S7 of male dorsally with setae on lateral lobes of distal process: 0 absent (Rightmyer 2004, Figs. 86–95); 1 present (Rightmyer 2004, Figs. 68–76).

89. Gonostylus of male with basal lobe: 0 absent (Rightmyer 2004, Fig. 128B); 1 present (Rightmyer 2004, Fig. 129).

90. Penis laterally with fleshy lobe (not to be confused with the much larger penis valve): 0 absent (Rightmyer 2004, Fig. 142); 1 present (Rightmyer 2004, Fig. 141).

**Appendix II: Supplementary figures and tables**

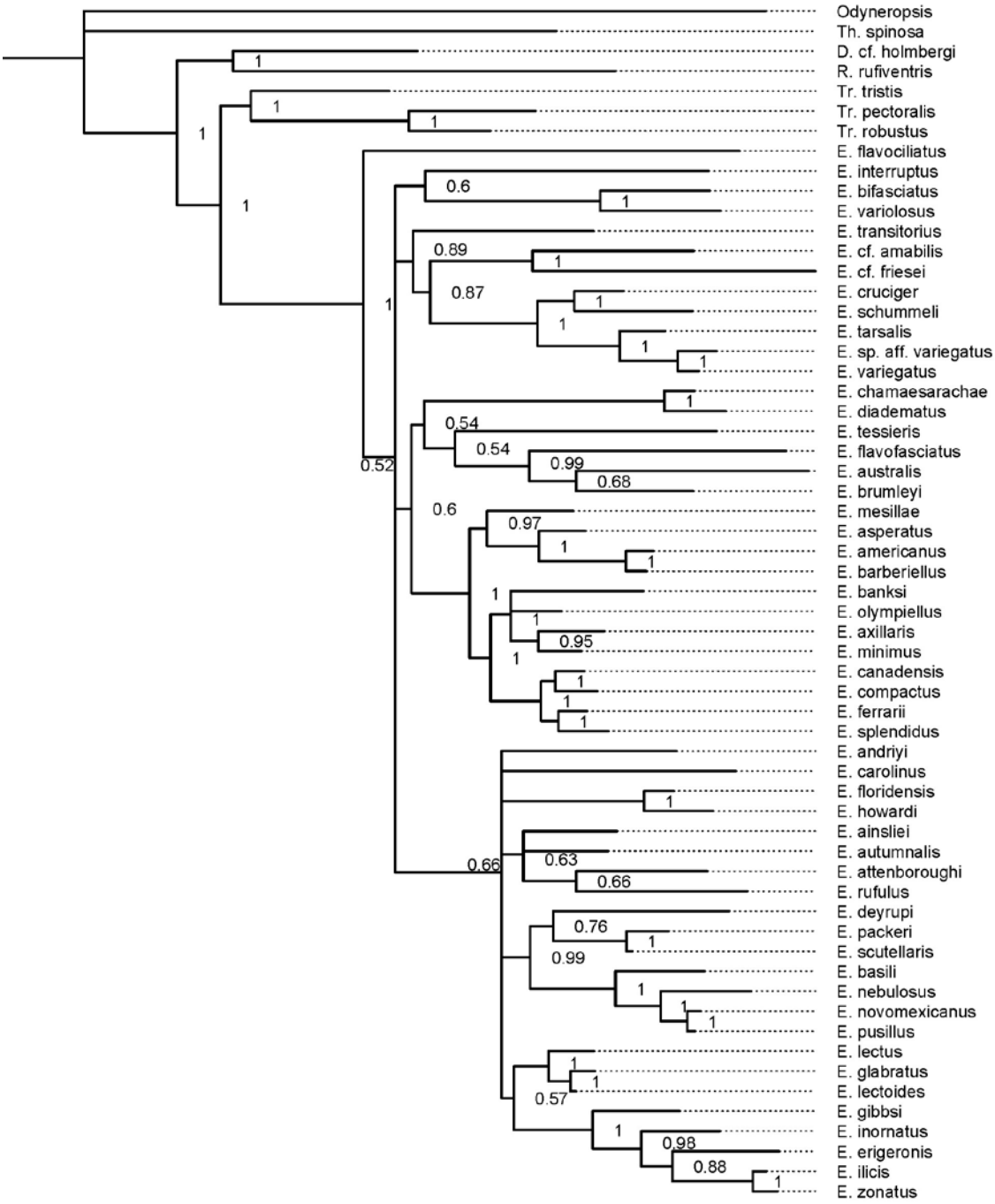


**Figure S1.** Undated phylogeny of *Epeolus* (based on the combined dataset of molecular sequences and morphological characters) obtained through phylogenetic analysis in MrBayes. Posterior probabilities are shown to the right of each node.

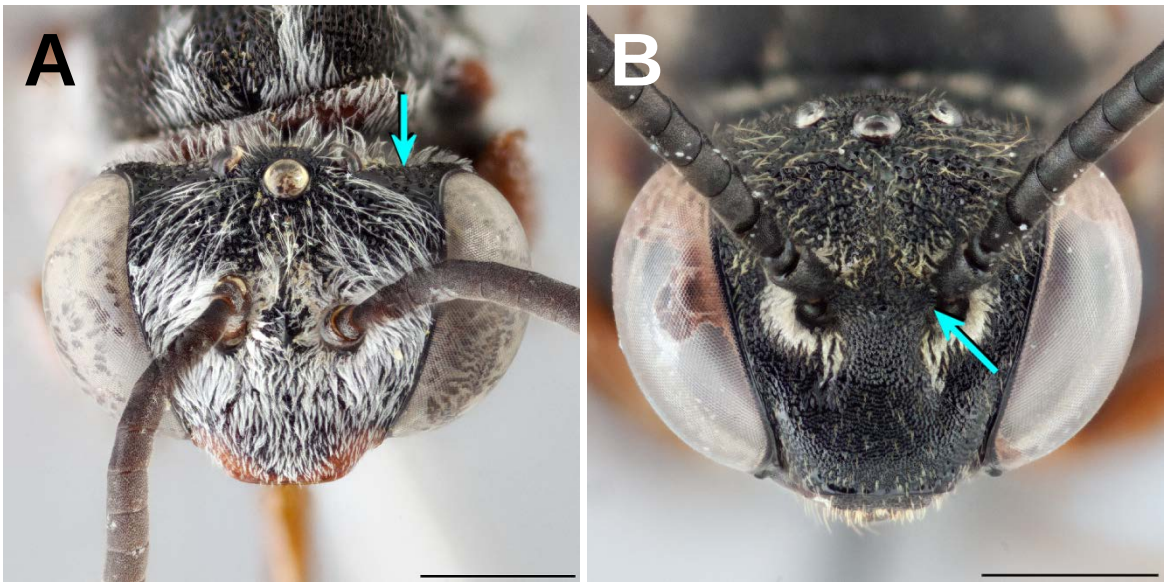


**Figure S2.** Head of female **A** *E.* cf. *amabilis* showing vertexal area with pair of distinct concavities between compound eye and lateral ocellus, and **B** *E. tarsalis* showing supraclypeal area expanded over the antennal socket. Scale bars 1 mm.

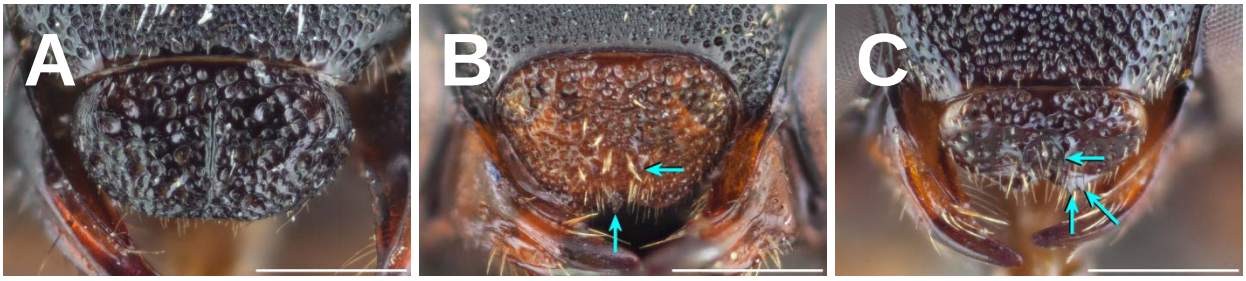


**Figure S3.** Labrum of female **A** *E.* cf. *friesei* without denticles, **B** *E. cruciger* showing pair of submedial denticles and apicomedial tooth, and **C** *E. diadematus* holotype showing pair of submedial denticles and two pairs of apical denticles. Scale bars 0.5 mm.

**Figure S4.** Clypeus of female *Triepeolus pectoralis* showing longitudinal impunctate line. Scale bar 0.5 mm.

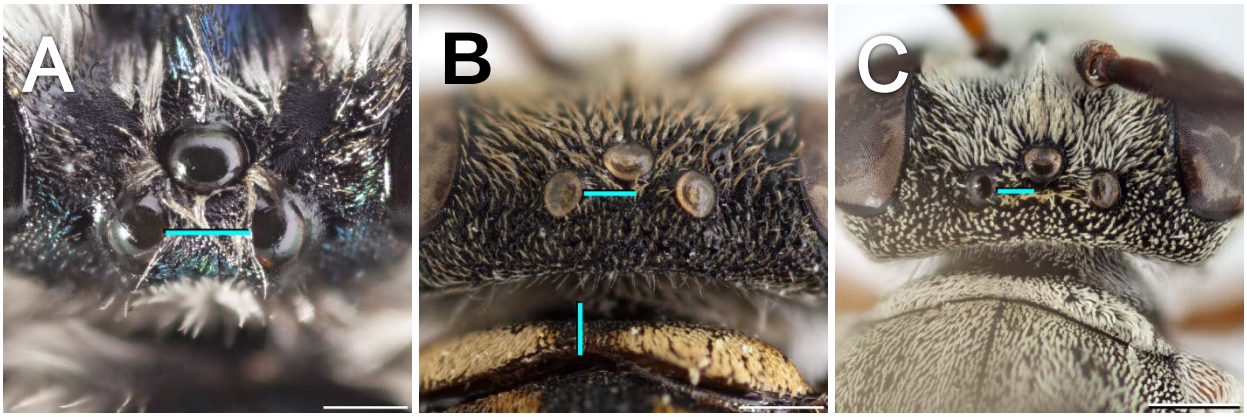


**Figure S5.** Head (in dorsal view) of **A** female *Thalestria spinosa* showing the distance between the lateral ocelli to be approximately 1 MOD, **B** female *E. transitorius* showing the distance between the lateral ocelli to be approximately 2 MOD and the length of the pronotal collar to be approximately 2/3 MOD, and **C** male *E. nebulosus* holotype showing the distance between the lateral ocelli to be approximately 3 MOD (blue lines = 1 MOD). Scale bars 0.5 mm.

**Figure S6.** Head (in posterior view) removed from female *Odyneropsis* (*Parammobates*) sp., in which the preoccipital ridge is absent. Scale bar = 1 mm.

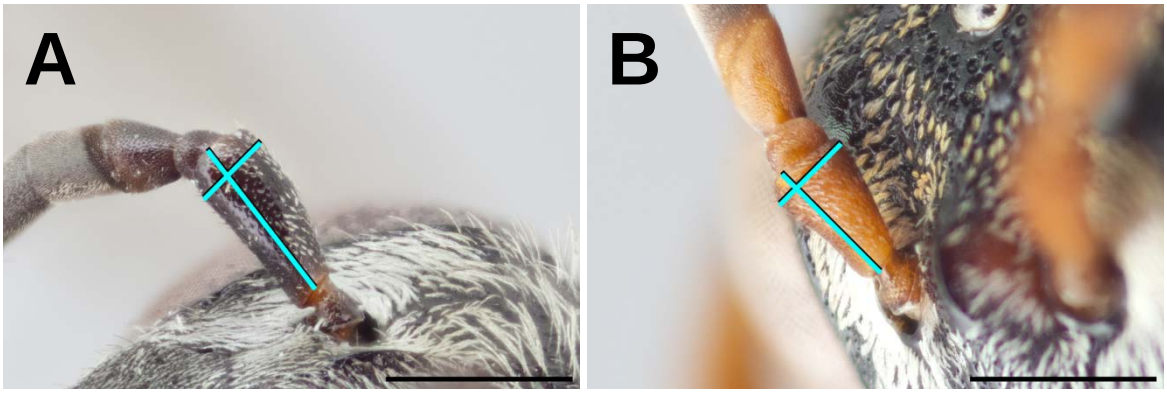


**Figure S7.** Antennae (basal portion) of female Epeolini spp. illustrating relative length to width of scape: **A** *Triepeolus pectoralis*, with the scape's greatest length >1.8 × greatest width, and **B** *E. variolosus*, with the scape's greatest length <1.7 × greatest width. Scale bars 0.5 mm.

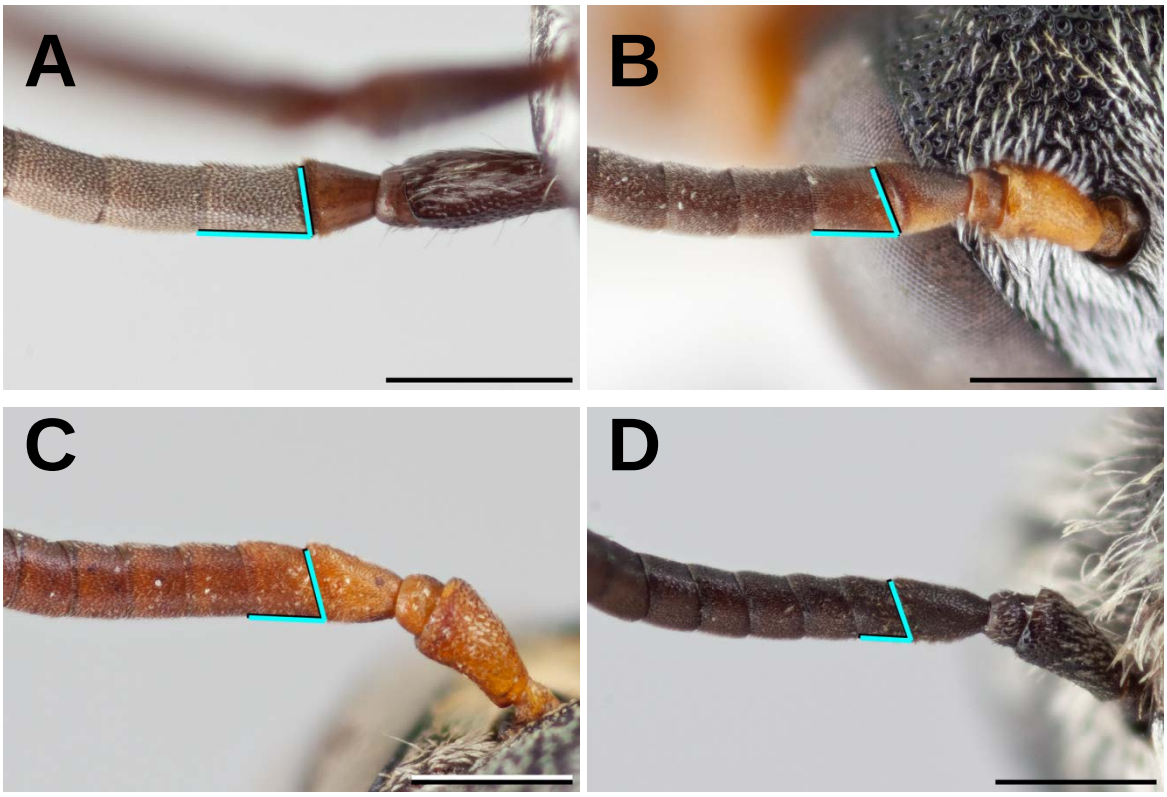


**Figure S8.** Antennae (basal portion) of male Epeolini spp. illustrating relative length to width of F2: **A** *Odyneropsis* (*Parammobates*) sp., with F2 much longer than wide, **B** *E. packeri* paratype, with F2 somewhat longer than wide, and **C** *E. variolosus*, with F2 as wide as long, or nearly so, and **D** *E. americanus*, with F2 wider than long. Scale bars 0.5 mm.

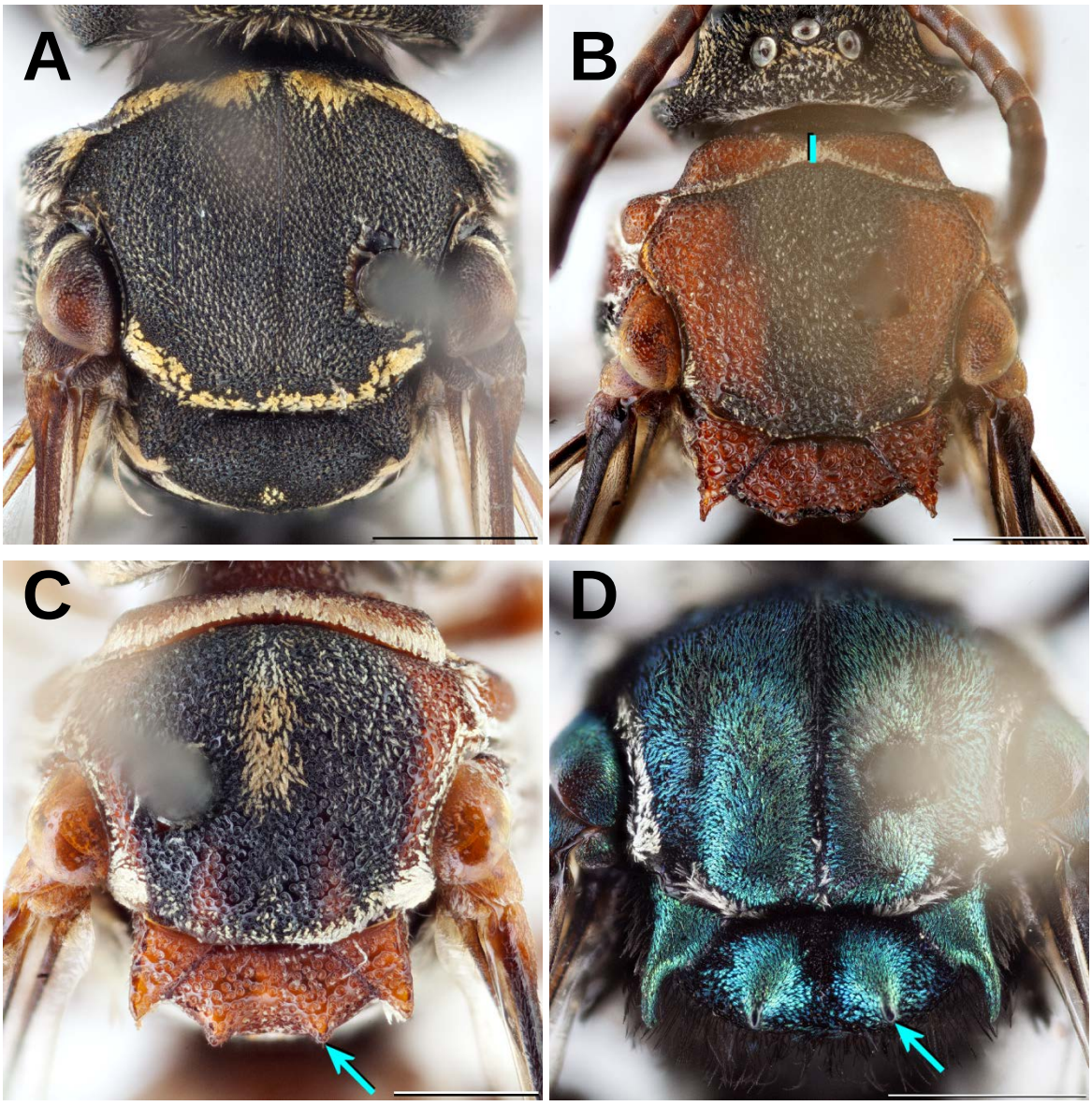


**Figure S9.** Mesosoma (in dorsal view) of female **A** *Doeringiella* cf. *holmbergi* showing the mesoscutum overhanging the pronotal collar (scale bar 1 mm), **B** *E. variolosus* showing the length of the pronotal collar to be approximately 1 MOD (blue line) (scale bar 1 mm), **C** *Rhinepeolus rufiventris* showing mesoscutellum with a pair of prominent mammiform tubercles (scale bar 1 mm), and **D** *Thalestria spinosa* showing mesoscutellum with a pair of prominent mammiform tubercles (scale bar 2 mm).

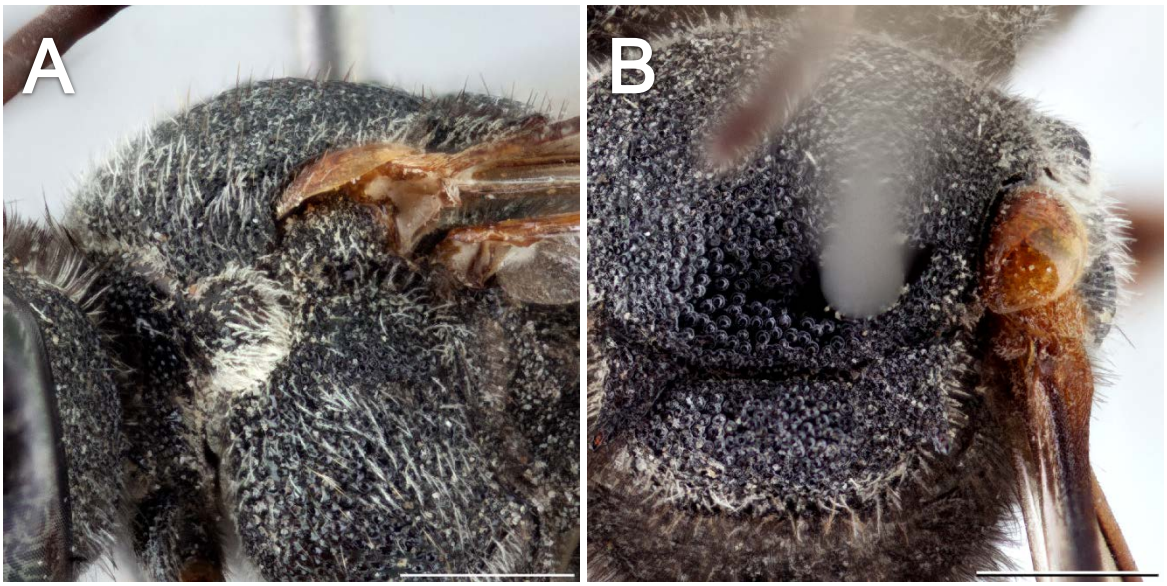


**Figure S10.** Mesosoma of female *E.* cf. *friesei* in **A** lateral view, showing mesoscutum with sparse and erect mixed pale and dark hairs, and **B** dorsal view, showing mesopleuron with sparse and erect mixed pale and dark hairs. Scale bars 1 mm.

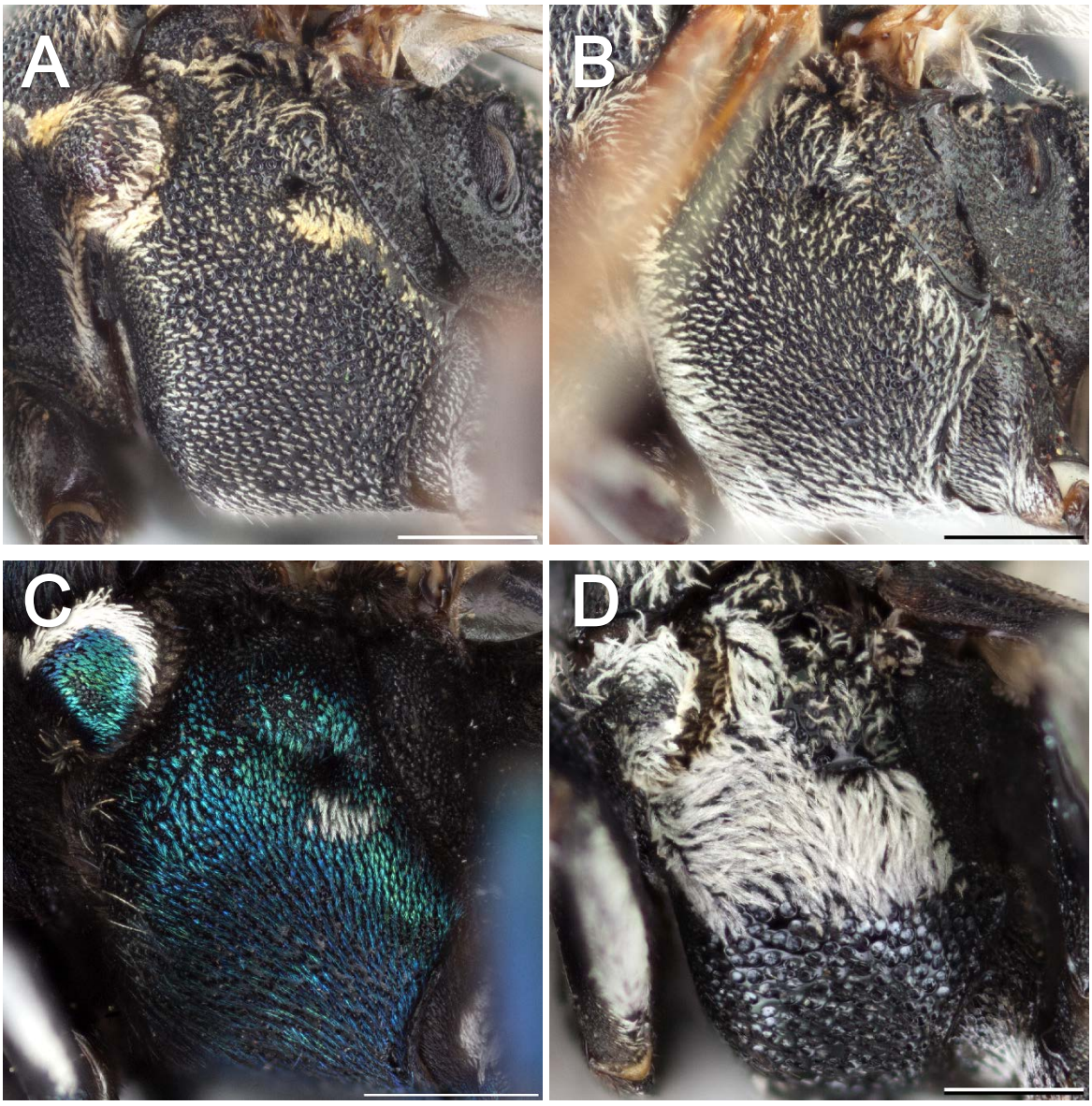


**Figure S11.** Mesopleuron (lateral view) of **A** female *Doeringiella* cf. *holmbergi*, which is covered in dense and very short pale tomentum (scale bar 0.5 mm), **B** male *Doeringiella* cf. *holmbergi*, which is more densely covered in pale tomentum than mesopleuron of female (scale bar 0.5 mm), **C** female *Thalestria spinosa*, which is densely covered in metallic blue-green tomentum except for the small patch of white tomentum below scrobe (scale bar 1 mm), and **D** female *Triepeolus tristis*, which is densely hairy in the upper half, except for beneath base of fore wing, and nearly bare in the ventrolateral half (scale bar 0.5 mm).

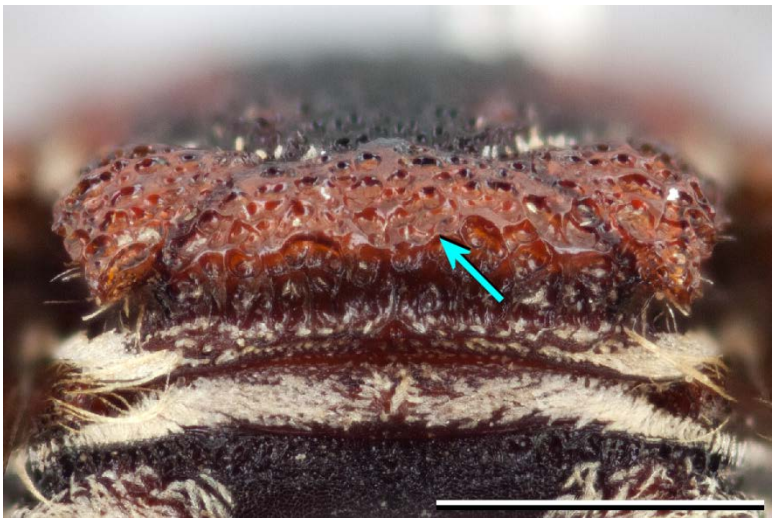

**Figure S12.** Mesoscutellum (in posterior view) of female *E. variolosus*, which has a distinct ridge overhanging its posterior surface. Scale bar 1 mm.

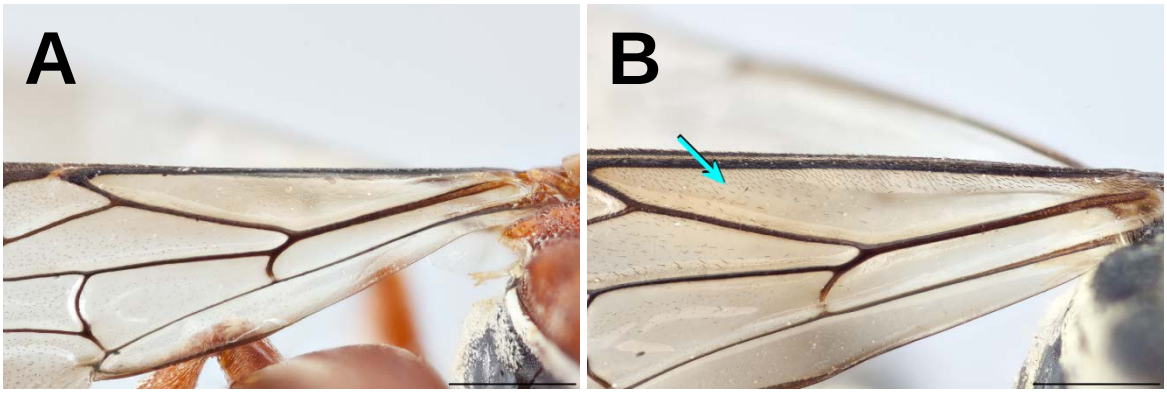


**Figure S13.** Left fore wing of female **A** *Rhinepeolus rufiventris*, showing radial cell with virtually no hairs, and **B** *Triepeolus robustus*, showing radial cell with hairs abundant in costal half, virtually none along M+Cu. Scale bars 1 mm.

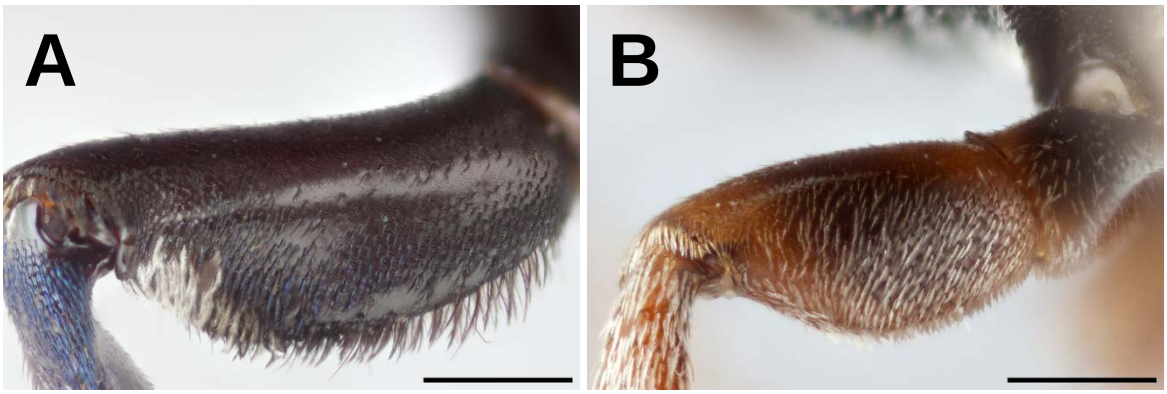


**Figure S14.** Left mesofemur of male **A** *Thalestria spinosa*, showing long setae on ventral surface, and **B** *E. schummeli*, showing comparatively short setae on ventral surface. Scale bars 0.5 mm.

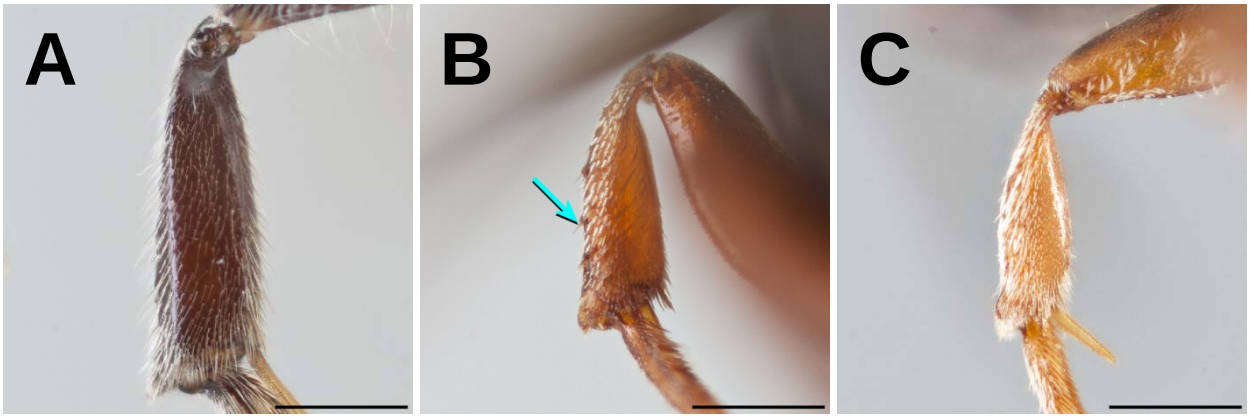


**Figure S15.** Left mesotibia (in posterior view) of female **A** *Odyneropsis* (*Parammobates*) sp., which lacks thick, spine-like setae and is covered in simple, uniform hairs, **B** *Triepeolus pectoralis*, which has abundant spine-like setae among the more numerous finer hairs, and **C** *E. minimus*, which has few thick, spine-like setae among the more numerous finer hairs. Scale bars 0.5 mm.


**Figure S16.** Left metatibia of female **A** *E. splendidus* paratype, with differentiated bases of spine-like setae not enlarged, and **B** *E. flavociliatus*, without differentiated bases of spine-like setae. Scale bars 0.5 mm.

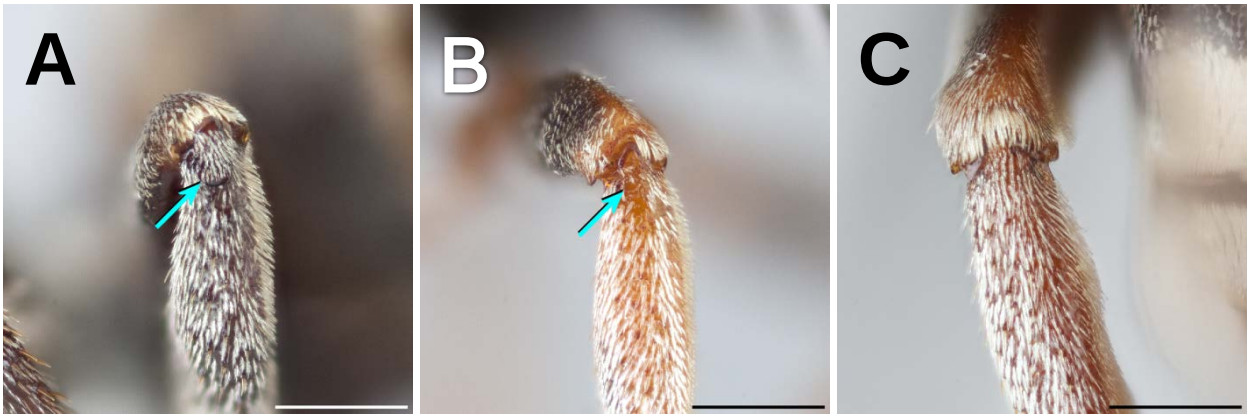


**Figure S17.** Left metatibia of female **A** *Doeringiella* cf. *holmbergi*, in which the basitibial plate is fully outlined by a carina, **B** *Triepeolus pectoralis*, in which the basitibial plate is partially outlined by a carina, and **C** *E. schummeli*, in which the basitibial plate is absent/indistinct from the rest of the tibia. Scale bars 0.5 mm.


**Figure S18.** Metasoma (in dorsal view) of female **A** *Odyneropsis* (*Parammobates*) sp., with pale pubescence limited to the basal half of T1, **B** *E.* cf. *friesei*, with pale pubescence is limited to the sides of T3 and T4, and **C** *E. tarsalis*, with basal fascia absent on T1 and apical fasciae widely interrupted medially on T1–T4. Scale bars 2 mm.

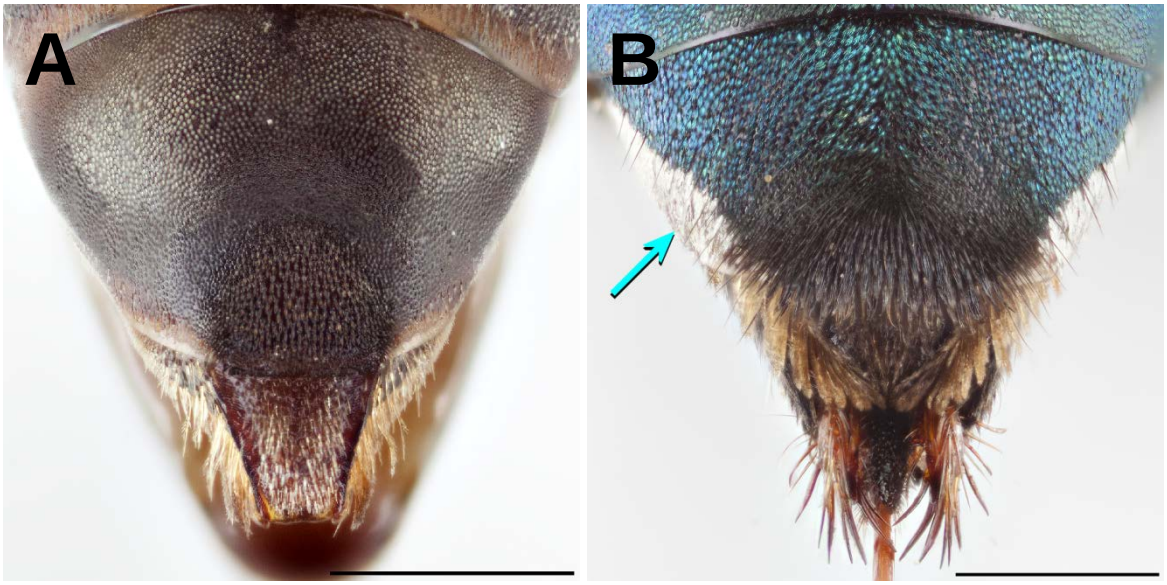


**Figure S19.** T5 of female **A** *Doeringiella* cf. *holmbergi*, with very short, minute pale hairs surrounding the ovate pseudopygidial area, and **B** *Thalestria spinosa*, with short patches of pale tomentum on either side of the pseudopygidial area, which does not have a distinct shape. Scale bars 1 mm.

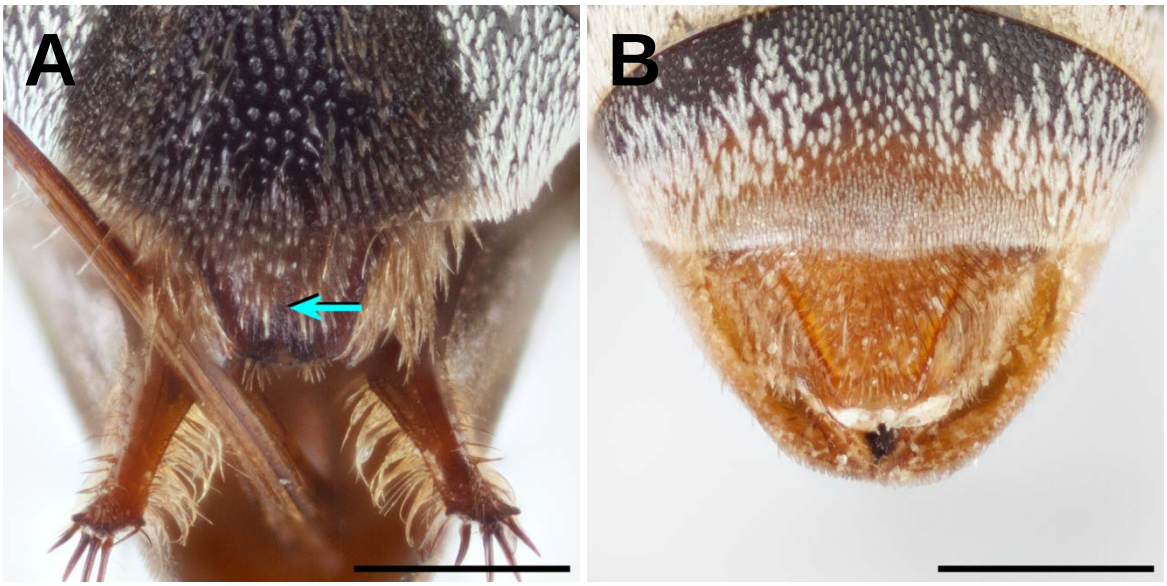


**Figure S20.** Pygidial plate of T6 of female **A** *Triepeolus pectoralis*, which has a medial longitudinal groove, and **B** *E. flavociliatus*, which lacks a medial longitudinal groove. Scale bars 0.5 mm.

**Figure S21.** Pygidial plate of female *Odyneropsis* (*Parammobates*) sp. (in posterior view) showing a pair of lateral enlarged triangular processes, which appear to be derived from both the lateral and ventral surfaces of T6. Scale bar 0.5 mm.


**Figure S22.** S6 of female (in ventral view) of **A** *E.* cf. *friesei*, in which the lobe-like disc is evenly convex and apical lateral processes bear numerous minute, pointed setae, **B** *E. chamaesarachae* paratype¸ in which the lobe-like disc is with distinctly emarginated apically, and **C** *E. deyrupi* paratype, in which the lobe-like disc is slightly emarginated apically. Scale bars 0.5 mm.

**Table S1.** A list of Epeolini and colletid specimens from which new DNA sequences were obtained. Details are given with regard to specimen collection, identification, and vouchering. For previously published sequences used in phylogenetic analysis, see Table S2.

| Genus | Species | Voucher number | DNA barcode | Sample ID (if barcoding attempted) | GenBank accession no. (for barcoded specimens) | Specimen repository | Collection information | Sex |
|---|---|---|---|---|---|---|---|---|
| *Epeolus* | *ainsliei* | LP001 | BOLD:ACZ1957 | CCDB-30345 B12 | MH089843 | PCYU | Canada: Ontario: Rondeau Provincial Park (42.2814°N; 81.8427°W) (Beach Access #10, near Visitor Centre), 08.viii.2017, R. Ferrari | ♂ |
| *Epeolus* | *asperatus* | LP002 | BOLD:ACZ2142 | CCDB-24580 B09 | MH090008 | PCYU | USA: California: Robert J. Bernard Biological Field Station (34.1083°N; 117.7100°W) (Claremont, Los Angeles County), 13.iv.2016, T.M. Onuferko | ♂ |
| *Epeolus* | *autumnalis* | TO001 | None | N/A | Not yet available | T.M. Onuferko Collection | Canada: Ontario: Black Creek Parkland (43.7703°N; 79.5153°W) (Toronto), 23.ix.2015, T.M. Onuferko | ♀ |
| *Epeolus* | *basili* | LP003 | None | N/A | Not yet available | PCYU | USA: Arizona: Blue Sky Road (4 mi E Willcox, Cochise County), 05.ix.2015, T.M. Onuferko Ex Psorothamnus scoparius? | ♀ |
| *Epeolus* | *bifasciatus* | LP004 | BOLD:ADD5310 | CCDB-24580 B01 | MH089986 | PCYU | Canada: Ontario: Point Pelee National Park (Cactus Field) (Essex County), 27.vii.2016, T.M. Onuferko | ♂ |
| *Epeolus* | *brumleyi* | LP005 | BOLD:ACZ9234 | CCDB-24580 B11 | MH089901 | PCYU | USA: Arizona: Hwy 80 (31.4450°N; 109.4722°W) (~8 mi NE Douglas, Cochise County), 10.v.2016, T.M. Onuferko Ex Chamaesaracha | ♀ |
| *Epeolus* | *canadensis* | LP006 | None | N/A | N/A | PCYU | USA: New Mexico: NM-15 Scenic (Gila National Forest), 17.viii.2015, T.M. Onuferko | ♂ |
| *Epeolus* | cf. *amabilis* | MK001 | BOLD:ABA3246 | CCDB-30345 A03 | Not yet available | M. Kuhlmann Collection | Republic of South Africa: Northern Cape: W Nieuwoudtville Flower Reserve (31.3200°S; 19.0800°E), 03.ix.2002, M. Kuhlmann | ♀ |
| *Epeolus* | cf. *friesei* | LP007 | BOLD:ABX3792 | CCDB-15279 G02 | Not yet available | PCYU | Republic of South Africa: Western Cape: Rietvlei (32.1461°S; 18.7725°E), 22.ix.2011, L. Packer | ♀ |
| *Epeolus* | *chamaesarachae* | LP008 | None | N/A | N/A | PCYU | USA: Arizona: Geronimo Trail at Sycamore Creek (31.4432°N; 109.1390°W) (Cochise County), 28.viii.2016, L. Packer Ex Baccharis | ♀ |
| *Epeolus* | *compactus* | LP009 | None | CCDB-24583 H10 | N/A | PCYU | USA: New Mexico: NM-146 (N Hachita, Grant County), 30.iv.2016, T.M. Onuferko Ex Sphaeralcea | ♂ |
| *Epeolus* | *cruciger* | MK002 | None (partial sequence only) | CCDB-30345 A07 | Not yet available | M. Kuhlmann Collection | UK: Hayling Island (SE corner) (50.7750°N; 0.9378°W), 01.vii.2008, M. Kuhlmann | ♀ |
| *Epeolus* | *ferrarii* | LP010 | None | N/A | N/A | PCYU | USA: New Mexico: 47 km S Animas (31.5438°N; 108.8757°W) (Co Rd C001), 30.viii.2015, R. Ferrari and T.M. Onuferko | ♂ |
| *Epeolus* | *flavociliatus* | JS001 | BOLD:ADL3226 | CCDB-30346 A06 | Not yet available | J. Straka Collection | Tunisia: Kebili Governorate: Blidet (S Qibilī) (33.5833°N; 8.8333°E), 01-02.iv.2006, J. Batelka and J. Straka | ♀ |
| *Epeolus* | *interruptus* | LP011 | None | N/A | N/A | PCYU | USA: Arizona: Geronimo Trail at Sycamore Creek (31.4432°N; 109.1390°W) (Cochise County), 28.viii.2016, L. Packer Ex Baccharis | ♀ |
| *Epeolus* | *lectoides* | LP012 | None | N/A | N/A | PCYU | Canada: Ontario: Point Pelee National Park (Cactus Field) (Essex County), 26.vii.2016, R. Ferrari and T.M. Onuferko | ♀ |

## Table S1 continued…

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Epeolus* | *lectus* | LP013 | None | N/A | N/A | PCYU | USA: Colorado: Bellvue (40.6882°N; 105.3070°W) (N Cache La Poudre River and E Gordon Creek, Larimer County), 28.vii.2015, A.T. and T.M. Onuferko | ♀ |
| *Epeolus* | *mesillae* | LP014 | BOLD:AAF0161 | CCDB-24580 B05 | MH089889 | PCYU | USA: California: Tipton Road (33.9079°N; 116.6510°W) (~1.4 mi SW Whitewater, Riverside County), 26.iii.2016, T.M. Onuferko | ♀ |
| *Epeolus* | *minimus* | LP015 | None | N/A | N/A | PCYU | USA: Colorado: Denver (Denver County), 15.vi.2017, T.M. Onuferko Ex Sphaeralcea | ♂ |
| *Epeolus* | *olympiellus* | LP016 | None | N/A | N/A | PCYU | Canada: British Columbia: Mount Tolmie Park (Victoria), 2015, S. McCann | ♂ |
| *Epeolus* | *pusillus* | LP017 | None | N/A | N/A | PCYU | USA: Florida: Heckscher Dr (Jacksonville), 25.ix.2016, T.M. Onuferko | ♂ |
| *Epeolus* | *schummeli* | PB001 | BOLD:ACD1345 | CCDB-30346 A08 | Not yet available | P. Bogusch Collection | Hungary: Bács-Kiskun County: Alsóadacsi temető (cemetery) (46.9383°N; 19.3201°E), 07.vi.2013, D. Banda, P. Bogusch, and J. Straka | ♂ |
| *Epeolus* | sp. aff. *variegatus* | MK003 | BOLD:ADI9219 | CCDB-30345 D04 | Not yet available | M. Kuhlmann Collection | Kazakhstan: Almaty Region: 10 km E Osinovka (45.8111°N; 80.7722°E) (Straßenrand), 19.vii.2002, M. Kuhlmann | ♀ |
| *Epeolus* | *splendidus* | LP018 | BOLD:ACX0474 | CCDB-22013 E11 | MH089954 | PCYU | USA: Arizona: Catalina Hwy (32.3631°N; 110.7137°W) (Santa Catalina Mountains, Coronado National Forest), 29.v.2015, A.T. Onuferko | ♀ |
| *Epeolus* | *tarsalis* | MK004 | BOLD:ABW4287 | CCDB-30345 A01 | Not yet available | M. Kuhlmann Collection | Netherlands: South Holland: Kwade Hoek, 23.viii.2005, M. Kuhlmann | ♂ |
| *Epeolus* | *transitorius* | MK005 | BOLD:ACD1277 | CCDB-30345 A05 | Not yet available | M. Kuhlmann Collection | Greece: Thessaly: Platania, 6.8.2005, K. Standfuss | ♀ |
| *Epeolus* | *transitorius* | MK006 | None | N/A | N/A | M. Kuhlmann Collection | Greece: Thessaly: Platania, 21.viii.2005, L. Standfuss | ♂ |
| *Epeolus* | *variolosus* | LP019 | BOLD:ABW4286 | CCDB-15259-H05 | Not yet available | PCYU | Argentina: Chaco Province: Chaco National Park (26.8875°S; 59.6224°W), 20.iv.2008, A. Taylor | ♀ |
| *Odyneropsis* | sp. | LP020 | BOLD:AAH6452 | CCDB-03756 B10 | Not yet available | PCYU | Colombia: Departamento del Chocó: Parque Nacional Natural Utría (Centro de Visitantes) (6.0200°N; 77.3500°W), 30.vi.-05.vii.2000, Brown and Campos | ♂ |
| *Rhinepeolus* | *rufiventris* | 06728C04-BOL | BOLD:AAO1283 | 06728C04-BOL | Not yet available | BBSL | Bolivia: Santa Cruz Department: 11 km N Boyuibe (20.3958°S; 63.3703°W), 04.iii.1999, M.E. Irwin and F.D. Parker | ♀ |
| *Thalestria* | *spinosa* | LP021 | BOLD:AAI0941 | ARG-09809-56 | Not yet available | PCYU | Argentina: Corrientes Province: Mburucuyá (28.0206°S; 58.0345°W), 29.i.2010, N. Veiga | ♀ |
| *Triepeolus* | *pectoralis* | TO002 | None | N/A | N/A | T.M. Onuferko Collection | Canada: Ontario: High Park (43.6532°N; 79.4599°W) (Toronto), 19.viii.2017, T.M. Onuferko | ♂ |
| *Triepeolus* | *pectoralis* | CCDB-25141 C05 | BOLD:ADE0528 | CCDB-25141 C05 | Not yet available | RSKM | Canada: Ontario: North Gower (45.0970°N; 75.7480°W), 23.viii.2012, I. Naujokaitis-Lewis | ♂ |
| *Triepeolus* | *tristis* | LP022 | BOLD:ADI5993 | CCDB-30345 C11 | Not yet available | PCYU | Macedonia: Skopje Statistical Region: Skopje, 25.vi.2016, L. Correia da Rocha Filho | ♀ |
| *Colletes* | *americanus* | LP023 | BOLD:AAE9723 | CCDB-28238 G08 | Not yet available | PCYU | Canada: Ontario: Albion Hills Conservation Area (Caledon) (43.9280°N; 79.8300°W), 21.viii.2012, S. Dumesh | ♂ |

## Table S1 continued…

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Colletes* | *californicus* | LP024 | BOLD:ABZ4529 | CCDB-24580 C09 | Not yet available | PCYU | USA: California: Robert J. Bernard Biological Field Station (34.1083°N; 117.7100°W) (Claremont, Los Angeles County), 13.iv.2016, T.M. Onuferko | ♀ |
| *Colletes* | *californicus* | KJH.86 | BOLD:ABZ4529 | KJH.86 | Not yet available | University of California, San Diego | USA: California: San Diego National Wildlife Refuge Otay-Sweetwater Unit, 24.iii.2011, K. James Hung | ♀ |
| *Colletes* | cf. *timberlakei* | LP025 | None | N/A | N/A | PCYU | USA: Colorado: Bellvue (40.6882°N; 105.3070°W) (N Cache La Poudre River and E Gordon Creek, Larimer County), 28.vii.2015, A.T. and T.M. Onuferko Ex Dalea | ♀ |
| *Colletes* | cf. *timberlakei* | LP026 | BOLD:ACZ9863 | CCDB-28238 A03 | Not yet available | PCYU | USA: Colorado: Bellvue (40.6882°N; 105.3070°W) (N Cache La Poudre River and E Gordon Creek, Larimer County), 28.vii.2015, A.T. and T.M. Onuferko Ex Dalea | ♀ |
| *Colletes* | *clypeonitens* | LP027 | None | N/A | N/A | PCYU | USA: California: Tipton Road (33.9079°N; 116.6510°W) (~1.4 mi SW Whitewater, Riverside County), 26.iii.2016, T.M. Onuferko Ex Larrea | ♂ |
| *Colletes* | *clypeonitens* | 00-CA-2254 | BOLD:AAR9974 | 00-CA-2254 | Not yet available | BBSL | USA: California: Dumont Dunes (NW side) (San Bernardino County), 03.iv.2000, R. Andrus Ex Larrea tridentata | ♂ |
| *Colletes* | *compactus* | RF105 | BOLD:AAC3237 | CCDB-30346 F02 | Not yet available | PCYU | USA: Arizona: Onion Saddle (Cochise County), 30.viii.2015, R. Ferrari | ♂ |
| *Colletes* | *eulophi* | LP028 | BOLD:ABZ4837 | CCDB-30344 B07 | Not yet available | PCYU | USA: Arizona: Catalina Hwy (32.3631°N; 110.7137°W) (Santa Catalina Mountains, Coronado National Forest), 29.v.2015, A.T. Onuferko Ex Eriogonum | ♂ |
| *Colletes* | *eulophi* | LP029 | BOLD:ABZ4837 | CCDB-30344 C10 | Not yet available | PCYU | USA: Arizona: Flagstaff (35.1737°N; 111.6756°W) (Coconino County), 01-03.vi.2017, T.M. Onuferko and S. Tessier | ♀ |
| *Colletes* | *kincaidii* | LP030 | None | N/A | N/A | PCYU | Canada: Ontario: Navan (45.3982°N; 75.3623°W) (Caroltodd Dr & Whispering Willow Dr), 03.vii.2017, T.M. Onuferko | ♂ |
| *Colletes* | *kincaidii* | LP031 | BOLD:AAB6621 | CCDB-24580 B04 | Not yet available | PCYU | Canada: Ontario: Vaughan (Steeles Ave & Founders Rd) (43.7803°N; 79.5025°W), 09.vii.2015, R. Ferrari | ♀ |
| *Colletes* | *latitarsis* | TO003 | None | N/A | N/A | T.M. Onuferko Collection | Canada: Ontario: Derrydowns Park (43.7503°N; 79.5069°W) (Toronto), 05.vii.2016, T.M. Onuferko Ex Physalis heterophylla | ♀ |
| *Colletes* | *latitarsis* | RF26 | BOLD:AAI9271 | CCDB-28312 H09 | Not yet available | PCYU | Canada: Ontario: Derrydowns Park (43.7503°N; 79.5069°W) (Toronto), 05.vii.2016, R. Ferrari Ex Physalis heterophylla | ♀ |
| *Colletes* | *mitchelli* | RF31 | BOLD:ACF5111 | CCDB-24582 H05 | Not yet available | PCYU | USA: North Carolina: Kill Devil Hills (36.0015°N; 75.6646), 23.ix.2016, T.M. Onuferko | ♀ |
| *Colletes* | *nudus* | RF34 | BOLD:AAR9947 | CCDB-24580 A03 | Not yet available | PCYU | Canada: Ontario: Point Pelee National Park (Sanctuary) (Essex County), 26.vii.2016, R. Ferrari | ♂ |
| *Colletes* | *nudus* | RF54 | BOLD:AAR9947 | CCDB-30345 C02 | Not yet available | PCYU | Canada: Ontario: Rondeau Provincial Park (42.2668°N; 81.8438°W) (Beach Access #11), 08.viii.2017, R. Ferrari | ♀ |
| *Colletes* | *scopiventer* | LP032 | None | N/A | N/A | PCYU | USA: Arizona: Hwy 80 (31.4450°N; 109.4722°W) (~8 mi NE Douglas, Cochise County), 10.v.2016, T.M. Onuferko Ex Chamaesaracha | ♀ |

**Table S1 continued…**

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Colletes* | *scopiventer* | LP033 | BOLD:AAJ7578 | CCDB-28238 D12 | Not yet available | PCYU | USA: Arizona: 1 mi E Douglas (Cochise County), 27.viii.2007, H.T. Ngo | ♂ |
| *Colletes* | *simulans* | RF55 | BOLD:AAC0970 | CCDB-30345 G04 | Not yet available | PCYU | Canada: Ontario: Picton, 31.viii.2017, R. Ferrari | ♂ |
| *Colletes* | *tectiventris* | LP034 | BOLD:ACX1219 | CCDB-28238 A09 | Not yet available | PCYU | USA: Arizona: S Blue Sky Road (4 mi E Willcox, Cochise County), 30.viii.2015, J.S. Francis | ♂ |
| *Colletes* | *willistoni* | RF33 | BOLD:ACC7841 | CCDB-24580 A01 | Not yet available | PCYU | Canada: Ontario: Point Pelee National Park (41.9340°N; 82.5170°W) (West Beach) (Essex County), 27.vii.2016, R. Ferrari | ♂ |
| *Colletes* | *wootoni* | LP035 | BOLD:AAI9255 | CCDB-30344 B03 | Not yet available | PCYU | USA: New Mexico: S Animas (Co Rd C001), 30.viii.2015, T.M. Onuferko | ♂ |

**Table S2.** A list of genes used to construct phylogenies for *Epeolus* and *Colletes*, and the corresponding source specimens for new sequences (vouchering details are given in Table S1) or GenBank accession numbers for previously published sequences.

| Genus | Species | 28S | COI | EF-1α | Opsin | Pol II | Wingless | Source for GenBank sequence(s) |
|---|---|---|---|---|---|---|---|---|
| *Doeringiella* | cf. *holmbergi* | GU244884 | Not available | GU245025 | GU245329 | GU245481 | GU245656 | Cardinal et al. (2010) |
| *Epeolus* | *ainsliei* | LP001 | MH089843 | LP001 | LP001 | LP001 | LP001 | Onuferko (2018) |
| *Epeolus* | *andriyi* | Not available | MH089972 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *asperatus* | LP002 | MH090008 | LP002 | LP002 | LP002 | LP002 | Onuferko (2018) |
| *Epeolus* | *attenboroughi* | Not available | MH089913 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *australis* | Not available | MH089930 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *autumnalis* | TO001 | MH089931 | TO001 | TO001 | TO001 | TO001 | Onuferko (2018) |
| *Epeolus* | *axillaris* | Not available | MH089840 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *barberiellus* | Not available | MH089915 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *basili* | LP003 | MH090001 | LP003 | LP003 | LP003 | LP003 | Onuferko (2018) |
| *Epeolus* | *bifasciatus* | LP004 | MH089986 | LP004 | LP004 | LP004 | LP004 | Onuferko (2018) |
| *Epeolus* | *brumleyi* | LP005 | MH089901 | LP005 | LP005 | LP005 | LP005 | Onuferko (2018) |
| *Epeolus* | *canadensis* | LP006 | MH089848 | LP006 | LP006 | LP006 | LP006 | Onuferko (2018) |
| *Epeolus* | *carolinus* | Not available | MH089997 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | cf. *amabilis* | MK001 | MK001 | MK001 | MK001 | MK001 | MK001 | N/A |
| *Epeolus* | cf. *friesei* | Not available | CCDB-15279 G02 | Not available | Not available | Not available | Not available | N/A |
| *Epeolus* | *chamaesarachae* | LP008 | MH089974 | LP008 | LP008 | LP008 | LP008 | Onuferko (2018) |
| *Epeolus* | *compactus* | LP009 | MH089882 | LP009 | LP009 | LP009 | LP009 | Onuferko (2018) |
| *Epeolus* | *cruciger* | MK002 | MK002 | MK002 | MK002 | MK002 | MK002 | N/A |
| *Epeolus* | *deyrupi* | Not available | MH090010 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *diadematus* | Not available | MH089940 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *erigeronis* | Not available | MH089872 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *ferrarii* | LP010 | MH089922 | LP010 | LP010 | LP010 | LP010 | Onuferko (2018) |
| *Epeolus* | *flavociliatus* | Not available | JS001 | Not available | Not available | Not available | Not available | N/A |
| *Epeolus* | *flavofasciatus* | Not available | MH089914 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *floridensis* | Not available | MH089877 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *gibbsi* | Not available | MH089845 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *glabratus* | Not available | MH089967 | Not available | Not available | Not available | Not available | Onuferko (2018) |

## Table S2 continued…

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Epeolus* | *howardi* | Not available | MH090011 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *ilicis* | Not available | MH090014 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *inornatus* | Not available | MH089908 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *interruptus* | LP011 | MH089961 | LP011 | LP011 | LP011 | LP011 | Onuferko (2018) |
| *Epeolus* | *lectoides* | LP012 | MH090009 | LP012 | LP012 | LP012 | LP012 | Onuferko (2018) |
| *Epeolus* | *lectus* | LP013 | MH089993 | LP013 | LP013 | LP013 | LP013 | Onuferko (2018) |
| *Epeolus* | *mesillae* | LP014 | MH089889 | LP014 | LP014 | LP014 | LP014 | Onuferko (2018) |
| *Epeolus* | *minimus* | LP015 | MH090003 | LP015 | LP015 | LP015 | LP015 | Onuferko (2018) |
| *Epeolus* | *nebulosus* | Not available | MH089896 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *novomexicanus* | Not available | MH089959 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *olympiellus* | LP016 | MH089905 | LP016 | LP016 | LP016 | LP016 | Onuferko (2018) |
| *Epeolus* | *packeri* | Not available | MH089990 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *pusillus* | LP017 | MH089868 | LP017 | LP017 | LP017 | LP017 | Onuferko (2018) |
| *Epeolus* | *rufulus* | Not available | MH089980 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *schummeli* | Not available | PB001 | Not available | KC798351 | Not available | Not available | Gerth et al. (2013) |
| *Epeolus* | *scutellaris* | GU244882 | MH089944 | GU245022 | AF344596 | GU245479 | GU245653 | Cardinal et al. (2010) (Onuferko 2018 for COI sequence) |
| *Epeolus* | sp. aff. *variegatus* | MK003 | MK003 | Not available | Not available | Not available | Not available | N/A |
| *Epeolus* | *splendidus* | LP018 | MH089954 | LP018 | LP018 | LP018 | LP018 | Onuferko (2018) |
| *Epeolus* | *tarsalis* | MK004 | MK004 | MK004 | MK004 | MK004 | MK004 | N/A |
| *Epeolus* | *tessieris* | Not available | MH089853 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Epeolus* | *transitorius* | Not available | MK005 | MK005 | MK006 | MK005 | MK005 | N/A |
| *Epeolus* | *variegatus* | GU244887 | Not available | GU244988 | HM211846 | GU245484 | GU245659 | Cardinal et al. (2010) |
| *Epeolus* | *variolosus* | GU244885 | CCDB-15259-H05 | GU245026 | GU245330 | GU245482 | GU245657 | Cardinal et al. (2010) |
| *Epeolus* | *zonatus* | Not available | MH089858 | Not available | Not available | Not available | Not available | Onuferko (2018) |
| *Odyneropsis* | sp. | GU244881 | CCDB-03756 B10 | GU245021 | GU245327 | GU245478 | GU245652 | Cardinal et al. (2010) |
| *Rhinepeolus* | *rufiventris* | GU244886 | 06728C04-BOL | GU245027 | GU245331 | GU245483 | GU245658 | Cardinal et al. (2010) |
| *Thalestria* | *spinosa* | GU244883 | LP021 | GU245024 | GU245328 | GU245480 | GU245655 | Cardinal et al. (2010) |
| *Triepeolus* | *pectoralis* | TO002 | CCDB-25141 C05 | TO002 | TO002 | TO002 | TO002 | N/A |
| *Triepeolus* | *robustus* | AY654547 | Not available | GU245023 | AF344634 | AY945170 | GU245654 | Cardinal et al. (2010) |
| *Triepeolus* | *tristis* | LP022 | LP022 | LP022 | LP022 | LP022 | LP022 | N/A |

## Table S2 continued…

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Callomelitta* | *antipodes* | AY654483 | JN603418 | AY585122 | DQ115563 | AY945105 | EF032907 | Almeida and Danforth (2009) for wingless, Danforth et al. (2006a) for 28S and Pol II, Danforth et al. (2006b) for EF-1α and Opsin, and Kayaalp et al. (2017) for COI sequence |
| *Colletes* | *americanus* | EF028569 | LP023 | Not available | Not available | Not available | Not available | Kuhlmann et al. (2009) |
| *Colletes* | *californicus* | Not available | KJH.86 | LP024 | Not available | LP024 | LP024 | N/A |
| *Colletes* | cf. *timberlakei* | LP025 | LP026 | LP025 | Not available | LP025 | LP025 | N/A |
| *Colletes* | *clypeonitens* | LP027 | 00-CA-2254 | LP027 | LP027 | LP027 | LP027 | N/A |
| *Colletes* | *collaris* | Not available | DQ085544 | Not available | Not available | Not available | Not available | Kuhlmann et al. (2007) |
| *Colletes* | *compactus* | DQ768531 | RF105 | RF105 | RF105 | RF105 | RF105 | Almeida and Danforth (2009) |
| *Colletes* | *eulophi* | Not available | LP029 | LP028 | LP028 | LP028 | LP028 | N/A |
| *Colletes* | *halophilus* | EF028596 | DQ085542 | Not available | Not available | Not available | Not available | Kuhlmann et al. (2009) (Kuhlmann et al. 2007 for COI sequence) |
| *Colletes* | *kincaidii* | LP030 | LP031 | LP030 | LP030 | LP030 | LP030 | N/A |
| *Colletes* | *latitarsis* | TO003 | RF26 | TO003 | TO003 | TO003 | TO003 | N/A |
| *Colletes* | *mitchelli* | Not available | RF31 | RF31 | RF31 | RF31 | RF31 | N/A |
| *Colletes* | *nasutus* | Not available | HM401158 | Not available | KC798345 | Not available | Not available | Gerth et al. (2013) (Schmidt et al. (2015) for COI sequence) |
| *Colletes* | *nudus* | RF54 | RF34 | RF54 | RF54 | RF54 | RF54 | N/A |
| *Colletes* | *scopiventer* | LP032 | LP033 | LP032 | LP032 | LP032 | LP032 | N/A |
| *Colletes* | *simulans* | DQ768533 | RF55 | RF55 | RF55 | RF55 | RF55 | Almeida and Danforth (2009) |
| *Colletes* | *tectiventris* | LP034 | LP034 | LP034 | LP034 | LP034 | LP034 | N/A |
| *Colletes* | *willistoni* | RF33 | RF33 | RF33 | RF33 | RF33 | RF33 | N/A |
| *Colletes* | *wootoni* | LP035 | LP035 | LP035 | LP035 | LP035 | LP035 | N/A |
| *Hemicotelles* | *ruizii* | DQ768527 | DQ872680 | DQ884638 | DQ884539 | Not available | DQ884790 | Almeida and Danforth (2009) |

**Table S3.** Matrix of morphological characters used in BI and MP analyses. Column headers indicate character numbers. Polymorphic character states are in square brackets. Question marks are used if a character state is unknown or a character is inapplicable to a particular taxon.

| | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Odyneropsis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 |
| *D.* cf. *holmbergi* | 1 | 1 | ? | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *R. rufiventris* | 1 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 0 |
| *Th. spinosa* | [0 1] | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| *Tr. pectoralis* | 1 | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Tr. robustus* | 1 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Tr. tristis* | 1 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *E. ainsliei* | 1 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 |
| *E.* cf. *amabilis* | 2 | 0 | 1 | 1 | ? | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. americanus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *E. andriyi* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. asperatus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. attenboroughi* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. australis* | 1 | 0 | 0 | 1 | ? | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *E. autumnalis* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. axillaris* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *E. banksi* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *E. barberiellus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *E. basili* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. bifasciatus* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. brumleyi* | 1 | 0 | 0 | 1 | ? | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. canadensis* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. carolinus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 |
| *E. chamaesarachae* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. compactus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. cruciger* | 1 | 0 | 0 | 1 | ? | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. deyrupi* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 1 |
| *E. diadematus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. erigeronis* | 1 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. ferrarii* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. flavociliatus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. flavofasciatus* | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. floridensis* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E.* cf. *friesei* | 2 | 1 | ? | 1 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. gibbsi* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. qlabratus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 1 |
| *E. howardi* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 |
| *E. ilicis* | 1 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. inornatus* | 1 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. interruptus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. lectoides* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 |
| *E. lectus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. mesillae* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. minimus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *E. nebulosus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3 | 1 | 1 | 0 | 0 |
| *E. novomexicanus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. olympiellus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *E. packeri* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 |
| *E. pusillus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. rufulus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. schummeli* | 0 | 0 | 0 | 1 | ? | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. scutellaris* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 |
| *E. splendidus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. tarsalis* | 1 | 0 | 0 | 1 | ? | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. tessieris* | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. transitorius* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *E. variegatus* | 1 | 0 | 0 | 1 | ? | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E.* sp. aff. *variegatus* | 1 | 0 | 0 | 1 | ? | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. variolosus* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |
| *E. zonatus* | 1 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |

## Table S3 continued…

| | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Odyneropsis* | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *D.* cf. *holmbergi* | 0 | 1 | 0 | 0 | 3 | ? | 0 | 7 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *R. rufiventris* | 1 | 2 | 0 | 1 | 5 | ? | 2 | 1 | 0 | ? | 1 | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Th. spinosa* | 0 | 1 | 0 | 0 | 6 | ? | 0 | 8 | 0 | ? | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Tr. pectoralis* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | [0 2] | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Tr. robustus* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | ? | 0 | 3 | 0 | 0 | [0 1] | 0 | 0 | 0 | 1 | 0 |
| *Tr. tristis* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *E. ainsliei* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E.* cf. *amabilis* | 0 | ? | 0 | 1 | 1 | 0 | 0 | 1 | ? | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | ? | 0 | 0 |
| *E. americanus* | 1 | 3 | 0 | 1 | 1 | 0 | 0 | 3 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. andriyi* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E. asperatus* | 1 | 3 | 0 | 1 | 1 | 0 | 0 | 3 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. attenboroughi* | 1 | 2 | 0 | 1 | 2 | ? | 0 | 4 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E. australis* | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *E. autumnalis* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *E. axillaris* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *E. banksi* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. barberiellus* | 1 | 3 | 0 | 1 | 1 | 0 | 0 | 3 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. basili* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *E. bifasciatus* | 0 | 2 | 1 | 2 | 0 | ? | 1 | 5 | 0 | ? | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *E. brumleyi* | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *E. canadensis* | 0 | 2 | 0 | 1 | 3 | ? | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. carolinus* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E. chamaesarachae* | 1 | 3 | 0 | 1 | 1 | 1 | 2 | 6 | 0 | ? | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *E. compactus* | 0 | 2 | 0 | 1 | 3 | ? | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. cruciger* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *E. deyrupi* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E. diadematus* | 1 | 3 | 0 | 1 | 1 | 1 | 2 | 6 | 0 | ? | 1 | 3 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *E. erigeronis* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | [0 1] |
| *E. ferrarii* | 1 | 2 | 0 | 1 | 3 | ? | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. flavociliatus* | 1 | 2 | 0 | 0 | 2 | ? | 3 | 4 | 0 | ? | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E. flavofasciatus* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *E. floridensis* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E.* cf. *friesei* | 0 | ? | 0 | 1 | 4 | ? | 0 | 0 | ? | ? | 1 | 3 | 0 | 0 | 0 | 0 | 0 | ? | 1 | 0 |
| *E. gibbsi* | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. glabratus* | 0 | 1 | 0 | 1 | 1 | 0 | 3 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | [0 1] |
| *E. howardi* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E. ilicis* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *E. inornatus* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *E. interruptus* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *E. lectoides* | 0 | 1 | 0 | 1 | 1 | 0 | 3 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | [0 1] |
| *E. lectus* | 0 | 1 | 0 | 1 | 1 | 0 | 3 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *E. mesillae* | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 4 | 0 | ? | 1 | 0 | 0 | 0 | [0 1] | 0 | 0 | 0 | 1 | 0 |
| *E. minimus* | 0 | 2 | 0 | 1 | [1 2] | 0 | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. nebulosus* | 0 | 1 | 0 | 1 | 2 | ? | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *E. novomexicanus* | 0 | 2 | 0 | 1 | [1 2] | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *E. olympiellus* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. packeri* | 0 | 1 | 0 | 1 | 0 | ? | 0 | 5 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E. pusillus* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *E. rufulus* | 0 | 2 | 0 | 1 | 2 | ? | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E. schummeli* | ? | 2 | 0 | 1 | 1 | 0 | 0 | 1 | ? | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *E. scutellaris* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *E. splendidus* | 1 | 2 | 0 | 1 | 3 | ? | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. tarsalis* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 5 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *E. tessieris* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *E. transitorius* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| *E. variegatus* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *E.* sp. aff. *variegatus* | 0 | ? | 0 | 1 | 1 | 0 | 0 | 1 | ? | ? | 1 | 0 | 0 | 0 | 0 | 1 | 1 | ? | 1 | 0 |
| *E. variolosus* | 0 | 2 | 1 | 2 | 0 | ? | 1 | 5 | 0 | ? | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *E. zonatus* | 0 | 2 | 0 | 1 | [0 1] | ? | 0 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |

## Table S3 continued…

| | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Odyneropsis* | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | [0 1] | 0 | 0 | ? | ? | ? | ? | ? | 0 |
| *D.* cf. *holmbergi* | 1 | ? | 1 | ? | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 3 | ? | 1 | ? | 0 | 1 | ? | 1 |
| *R. rufiventris* | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Th. spinosa* | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | ? | ? | ? | 3 | ? | ? | 4 |
| *Tr. pectoralis* | 1 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | [0 1] | 0 | 0 | 1 |
| *Tr. robustus* | 1 | ? | 1 | ? | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | [0 1] | 1 | [0 1] | 0 | 0 | 1 |
| *Tr. tristis* | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 3 | 1 | 0 | 1 | 2 |
| *E. ainsliei* | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | ? | 1 |
| *E.* cf. *amabilis* | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 1 | ? | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 3 |
| *E. americanus* | 1 | ? | 1 | ? | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 2 | [1 3] |
| *E. andriyi* | 0 | 1 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 2 |
| *E. asperatus* | 1 | ? | 1 | ? | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 2 | 3 |
| *E. attenboroughi* | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| *E. australis* | 1 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | [0 1] | 0 | [0 1] | 0 | 0 | 1 |
| *E. autumnalis* | 0 | 1 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | [0 1] | 0 | [0 1] | 1 | ? | 1 |
| *E. axillaris* | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 2 |
| *E. banksi* | 1 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 2 | 2 |
| *E. barberiellus* | 1 | ? | 1 | ? | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 2 | [1 3] |
| *E. basili* | 0 | 1 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *E. bifasciatus* | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | ? | ? | 0 | 1 | ? | 0 |
| *E. brumleyi* | 1 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | [1 2] | 0 | 0 | 2 | 0 | [0 1] | 0 | [0 1] | 0 | 0 | 1 |
| *E. canadensis* | 1 | ? | 1 | ? | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 4 | [0 1] | 1 | ? | [1 2] |
| *E. carolinus* | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | ? | 2 |
| *E. chamaesarachae* | 1 | ? | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 3 | 1 | 0 | 3 | 3 |
| *E. compactus* | 1 | ? | 1 | ? | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 1 | [0 1] | 1 | ? | [1 2] |
| *E. cruciger* | 1 | ? | 1 | ? | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 1 | 1 | ? | 3 |
| *E. deyrupi* | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | [0 1] | 0 | 3 | ? | 0 | ? | 1 | 1 | ? | 2 |
| *E. diadematus* | 1 | ? | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 3 | 1 | 0 | 3 | 3 |
| *E. erigeronis* | 1 | ? | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | [0 1] | 0 | 2 | 1 |
| *E. ferrarii* | 1 | ? | 1 | ? | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 2 | [0 1] | 1 | ? | [1 2] |
| *E. flavociliatus* | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | ? | 1 |
| *E. flavofasciatus* | 1 | ? | 0 | ? | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | [0 1] | [0 1] | 4 | [0 1] | 0 | 4 | 1 |
| *E. floridensis* | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | ? | 2 |
| *E.* cf. *friesei* | 1 | ? | 0 | ? | 2 | 0 | 0 | [0 1] | ? | 1 | 1 | 0 | 4 | ? | ? | ? | ? | ? | ? | 4 |
| *E. gibbsi* | 1 | ? | 2 | 1 | 0 | 0 | 0 | 0 | 0 | [1 2] | 0 | 0 | 2 | 0 | 0 | 2 | [0 1] | 0 | 2 | 1 |
| *E. glabratus* | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | ? | ? | 3 | 1 | ? | 4 |
| *E. howardi* | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | ? | 2 |
| *E. ilicis* | 1 | ? | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | [0 1] | 0 | 2 | [1 2] |
| *E. inornatus* | 1 | ? | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | [0 1] | 0 | 2 | [1 2] |
| *E. interruptus* | 1 | ? | 1 | ? | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 1 | 0 | 5 | 1 | 0 | 2 | 2 |
| *E. lectoides* | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 2 |
| *E. lectus* | [0 1] | 1 | 2 | [0 1] | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | [0 1] | 0 | 0 | 0 | 2 | 1 |
| *E. mesillae* | 1 | ? | 1 | ? | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 2 | 1 |
| *E. minimus* | 1 | ? | 0 | ? | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 1 | [0 1] | 0 | 0 | [1 2] |
| *E. nebulosus* | 0 | 1 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *E. novomexicanus* | 0 | 1 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | [0 1] | 0 | [0 1] | 0 | 0 | 1 |
| *E. olympiellus* | 1 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 3 |
| *E. packeri* | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 3 | ? | 0 | ? | 1 | 1 | ? | 2 |
| *E. pusillus* | 0 | 1 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | [0 1] | 0 | [0 1] | 0 | 0 | 1 |
| *E. rufulus* | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | ? | 1 |
| *E. schummeli* | 0 | 1 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 2 | 2 | 1 | ? | 3 |
| *E. scutellaris* | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | [0 1] | 0 | [0 1] | 0 | 4 | 1 |
| *E. splendidus* | 1 | ? | 1 | ? | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 5 | 0 | 1 | ? | 0 | 1 | ? | 1 |
| *E. tarsalis* | 1 | ? | 1 | ? | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | [2 3] | 0 | 0 | 3 | 1 | 1 | ? | 3 |
| *E. tessieris* | 1 | ? | 1 | ? | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 2 | 2 |
| *E. transitorius* | 0 | 0 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 3 |
| *E. variegatus* | 1 | ? | 0 | ? | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 1 | 1 | ? | 3 |
| *E.* sp. aff. *variegatus* | 1 | ? | 0 | ? | 0 | 0 | 0 | 0 | ? | 2 | 0 | 0 | 2 | 0 | 0 | 3 | 1 | 1 | ? | 3 |
| *E. variolosus* | 0 | 0 | 0 | ? | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 3 | ? | 1 | ? | ? | ? | ? | 0 |
| *E. zonatus* | 1 | ? | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | ? | 2 |

## Table S3 continued…

| | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Odyneropsis* | 0 | ? | 0 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 |
| *D.* cf. *holmbergi* | 1 | ? | 2 | ? | 1 | ? | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | ? | 0 |
| *R. rufiventris* | 1 | ? | 1 | 0 | 1 | ? | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | ? | 0 |
| *Th. spinosa* | 4 | ? | 1 | 0 | 4 | ? | 2 | 1 | 1 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 3 | ? | 0 |
| *Tr. pectoralis* | 1 | ? | 1 | 0 | 1 | ? | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | ? | 0 |
| *Tr. robustus* | 1 | ? | 1 | 0 | 1 | ? | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | ? | 0 |
| *Tr. tristis* | 2 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | ? | 0 |
| *E. ainsliei* | 1 | ? | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E.* cf. *amabilis* | 3 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 2 | ? | ? | ? | ? | ? | 0 | 0 | 2 | 0 | 1 |
| *E. americanus* | [1 3] | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. andriyi* | [1 2] | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | ? | 1 |
| *E. asperatus* | 3 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. attenboroughi* | 1 | ? | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. australis* | 1 | ? | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. autumnalis* | 1 | ? | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. axillaris* | [1 2] | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. banksi* | [1 2] | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | ? | 1 |
| *E. barberiellus* | [1 3] | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. basili* | 1 | ? | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. bifasciatus* | 0 | ? | 0 | ? | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. brumleyi* | 1 | ? | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. canadensis* | [1 2] | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. carolinus* | [1 2] | 1 | 0 | ? | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. chamaesarachae* | 3 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 |
| *E. compactus* | [1 2] | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. cruciger* | 3 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. deyrupi* | [1 2] | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 2 | 1 |
| *E. diadematus* | 3 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 |
| *E. erigeronis* | 1 | ? | 1 | 0 | 3 | ? | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. ferrarii* | [1 2] | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. flavociliatus* | 1 | ? | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. flavofasciatus* | 1 | ? | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. floridensis* | [1 2] | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E.* cf. *friesei* | 4 | ? | 0 | ? | 2 | 0 | 1 | 0 | 1 | 2 | ? | ? | ? | ? | ? | 0 | 0 | 2 | 0 | 1 |
| *E. gibbsi* | 1 | ? | 1 | 0 | 3 | ? | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | ? | 1 |
| *E. glabratus* | 4 | ? | 1 | 0 | 3 | ? | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. howardi* | [1 2] | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. ilicis* | [1 2] | 1 | 1 | 0 | 3 | ? | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. inornatus* | [1 2] | 1 | 1 | 0 | 3 | ? | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 |
| *E. interruptus* | 2 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. lectoides* | [1 2] | 1 | 1 | 0 | 3 | ? | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. lectus* | 1 | ? | 1 | 0 | 3 | ? | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. mesillae* | 1 | ? | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. minimus* | [1 2] | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. nebulosus* | 1 | ? | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | ? | 1 |
| *E. novomexicanus* | 1 | ? | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. olympiellus* | 3 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. packeri* | [1 2] | 0 | 0 | ? | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. pusillus* | 1 | ? | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. rufulus* | 1 | ? | 0 | ? | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | ? | 1 |
| *E. schummeli* | 3 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. scutellaris* | 1 | ? | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. splendidus* | 1 | ? | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 2 | 1 |
| *E. tarsalis* | 3 | 0 | 0 | ? | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 |
| *E. tessieris* | 2 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | ? | 1 |
| *E. transitorius* | 3 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. variegatus* | 3 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 |
| *E.* sp. aff. *variegatus* | 3 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | ? | ? | ? | ? | ? | 1 | 0 | 2 | 0 | 1 |
| *E. variolosus* | 0 | ? | 0 | ? | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |
| *E. zonatus* | [1 2] | 1 | 1 | 0 | 3 | ? | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 |

## Table S3 continued…

| | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Odyneropsis* | 0 | ? | 0 | 2 | 0 | 0 | ? | 0 | 0 | 0 | 0 |
| *D.* cf. *holmbergi* | 1 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *R. rufiventris* | 1 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Th. spinosa* | 1 | ? | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Tr. pectoralis* | 1 | ? | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Tr. robustus* | 1 | ? | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Tr. tristis* | 1 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *E. ainsliei* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E.* cf. *amabilis* | 2 | 1 | 1 | 2 | 2 | ? | ? | ? | ? | ? | ? |
| *E. americanus* | 2 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 1 | 1 | 1 |
| *E. andriyi* | 2 | ? | 1 | 2 | 2 | ? | 1 | 0 | 1 | 1 | ? |
| *E. asperatus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. attenboroughi* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. australis* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. autumnalis* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. axillaris* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. banksi* | 2 | ? | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. barberiellus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. basili* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. bifasciatus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 0 |
| *E. brumleyi* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. canadensis* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. carolinus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. chamaesarachae* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. compactus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. cruciger* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. deyrupi* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. diadematus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. erigeronis* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. ferrarii* | 2 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 1 | 1 | 1 |
| *E. flavociliatus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. flavofasciatus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. floridensis* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E.* cf. *friesei* | 2 | 1 | 1 | 2 | 2 | ? | ? | ? | ? | ? | ? |
| *E. gibbsi* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. glabratus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. howardi* | 2 | 0 | 1 | 2 | 2 | ? | ? | ? | ? | ? | ? |
| *E. ilicis* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. inornatus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. interruptus* | 2 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 1 | 1 | 0 |
| *E. lectoides* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. lectus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. mesillae* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. minimus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. nebulosus* | 2 | ? | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. novomexicanus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. olympiellus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. packeri* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. pusillus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. rufulus* | 2 | ? | 1 | 2 | 2 | ? | ? | ? | ? | ? | ? |
| *E. schummeli* | 2 | ? | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. scutellaris* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. splendidus* | 2 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 1 | ? | ? |
| *E. tarsalis* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. tessieris* | 2 | ? | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. transitorius* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E. variegatus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |
| *E.* sp. aff. *variegatus* | 2 | 0 | 1 | 2 | 2 | ? | ? | ? | ? | ? | ? |
| *E. variolosus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | ? |
| *E. zonatus* | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |